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Bothalia is vernoem ter ere van Generaal Louis Botha, eerste Eerste Minister en Minister van Landbou van die Unie van Suid-Afrika. Hierdie lyfblad van die Nasionale Botaniese Instituut, Pretoria, is gewy aan die bevordering van die wetenskap van plantkunde. Die hoofgebiede wat gedek word, is taksonomie, ekologie, anatomie en sitologie. Twee dele van die tydskrif en 'n indeks van die inhoud, outeurs en onderwerpe verskyn jaarliks.

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Vanaf Vol. 50 word een deel, bestaande uit twintig plate, jaarliks gepubliseer. 'n Volume bestaan uit twee dele. Die publikasie is beskikbaar in Afrikaans en Engels.

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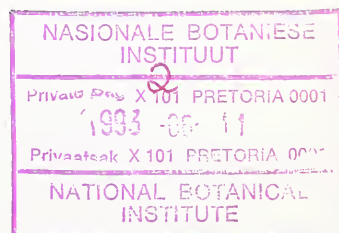


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CONTENTS — INHOUD

Volume 23,1

1. Studies in the Ericoideae (Ericaceae). XII. The placing of the genus <i>Blaeria</i> into synonymy under <i>Erica</i> ; nomenclatural and taxonomic changes for the southern African region. E.G.H. OLIVER	1
2. Studies in the Ericoideae (Ericaceae). XIII. Three new species of <i>Erica</i> from the southwestern Cape. E.G.H. OLIVER	9
3. The hepatics, <i>Symphyogyna podophylla</i> and <i>Pallavicinia lyellii</i> (Pallaviciniaceae) in southern Africa. S.M. PEROLD	15
4. A biosystematic study of <i>Pentameris</i> (Arundineae, Poaceae). N.P. BARKER	25
5. Studies in the Marchantiales (Hepaticae) from southern Africa. 1. The genus <i>Dumortiera</i> and <i>D. hirsuta</i> ; the genus <i>Lunularia</i> and <i>L. cruciata</i> . S.M. PEROLD	49
6. <i>Panicum simulans</i> (Paniceae, Poaceae), a new species from southern Africa and its leaf anatomy. L. SMOOK and R.P. ELLIS	59
7. Notes on African plants:	
Allisoniaceae. The hepatic, <i>Calycularia crispula</i> (Metzgeriales) reported from Malawi and Zambia. S.M. PEROLD	79
Asteraceae. An evaluation of Hutchinson's 'beetle-daisy' hypothesis. J.J. MIDGLEY	70
Fabaceae. <i>Vigna kokii</i> , a new species from southern Africa. B.J. PIENAAR	68
Fabaceae. Notes on the genus <i>Argyrobolium</i> (Crotalariaeae) including a new species from southern Africa. T.J. EDWARDS	77
Oxalidaceae. A new species of <i>Oxalis</i> from the western Cape. E.G.H. OLIVER	72
Pteridophyta—Adiantaceae. A new cytotype for <i>Acrostichum aureum</i> . J.P. ROUX	75
Rosaceae. Observations on <i>Cliffortia micrantha</i> . A.C. FELLINGHAM	65
Rosaceae. <i>Cliffortia fasciculata</i> , a superfluous name for <i>C. amplexistipula</i> . A.C. FELLINGHAM	67
8. First report on the presence of <i>Enterobryus</i> species (Trichomycetes: Eccliniales) in South Africa and the description of three new species. G.J.M.A. GORTER	85
9. Mycorrhizal status of plants growing in the Cape Floristic Region, South Africa. N. ALLSOPP and W.D. STOCK	91
10. Pollen morphology of <i>Curroria</i> , <i>Mondia</i> , <i>Socotranthus</i> and <i>Stomatostemma</i> (Periplocaceae). R.L. VERHOEVEN and H.J.T. VENTER	105
11. Dynamics of the forest vegetation of the Umtiza Nature Reserve, East London. J.J. MIDGLEY and P.N. GOBETZ	111
12. The vegetation of the northeastern Orange Free State, South Africa: physical environment and plant communities of the Ea land type. H.C. ECKHARDT, N. VAN ROOYEN and G.J. BREDENKAMP	117
13. The vegetation of the southern Langeberg, Cape Province. 1. The plant communities of the Boosmansbos Wilderness Area. D.J. MCDONALD.....	129
14. The vegetation of the southern Langeberg, Cape Province. 2. The plant communities of the Marloth Nature Reserve. D.J. MCDONALD	153



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Studies in the Ericoideae (Ericaceae). XII. The placing of the genus *Blaeria* into synonymy under *Erica*; nomenclatural and taxonomic changes for the southern African region

E.G.H. OLIVER*

Keywords: *Blaeria*, *Erica*, nomenclature, southern Africa, taxonomy

ABSTRACT

The reduction of the genus *Blaeria* to synonymy under *Erica* requires the publication of six new combinations and three new names for the nine taxa occurring in southern Africa. Four species are reduced to synonymy. Diagnostic features and distribution maps are provided.

UITTREKSEL

Die plasing van die genus *Blaeria* in sinonimie onder *Erica* vereis die publiserings van ses nuwe kombinasies en drie nuwe name vir die nege taksons wat in suidelike Afrika voorkom. Vier spesies word in sinonimie geplaas. Diagnostiese kenmerke en verspreidingskaarte word voorsien.

INTRODUCTION

In a forthcoming paper (Oliver in press A) the generic relationship between *Blaeria* L. and *Erica* L. will be discussed in detail. The former genus has been maintained separate from *Erica* since 1753 on the single character difference of four as opposed to eight stamens.

Problems arose with several species in both genera having a variable number of stamens or even numbers not included within the circumscription of their genera. Depending on the stamen complement found in the flowers examined, one could identify some material as either belonging to *Blaeria* or to *Erica*. Problem species in this respect are *Erica filiformis* Salisb., *E. esterhuyseniae* Compton and *E. pleiotricha* S. Moore in which 8- and 4-stamened flowers exist. In several other species the stamen number varies from 5 to 8.

With the sinking of the genus *Philippia* into *Erica* (Oliver 1987a, 1988, 1989) several additional species from tropical Africa having variable numbers of stamens were introduced into the problem. These are: *E. nyassana* (Alm & Fries) E.G.H. Oliver with only 4 stamens, very occasionally 5; *E. hexandra* (S. Moore) E.G.H. Oliver with 6, but 7 or 8 in some or all flowers; *E. mannii* (Hook. f.) Beentje has 6 stamens but with 5, 7 or 8 in some flowers. Several Madagascan species, not yet transferred to *Erica*, have also compounded the problem; *Philippia humbertii* H. Perrier with 3 or 4 stamens, sometimes 6 and *P. gracilis* (Benth.) H. Perrier with 4–8 stamens.

The genus *Blaeria* contains approximately 16 species, all occurring in Africa. In the southern African region the nine species are confined to the Cape. They can be placed in several groups of related species, with each group showing more affinities to different sections within *Erica*

than to the other groups within *Blaeria*, including those from tropical Africa.

It is postulated (Oliver in press A) that *Blaeria* is an unnatural genus with clear indications of being polyphyletic. On the grounds of polyphyletic and the complete transition between the two genera in the only differentiating character in certain species, it was decided to reduce the genus *Blaeria* to synonymy under *Erica*. This decision is formalised in this paper for the species occurring in the southern African region. At this stage it is not possible to deal with the nomenclatural changes necessary for the tropical African species because of the instability of their taxonomy and of several nomenclatural synonyms within *Erica*.

1. *Erica barbigeroides* E.G.H. Oliver, nom. nov.

Blaeria revoluta Bartl.: 650 (1832), non *Erica revoluta* (H. Bol.) L.E. Davidson (1985); Klotzsch: 663 (1833); Klotzsch: 222 (1838); Benth.: 698 (1839); N.E. Br.: 326 (1905). *Blairia revoluta* (Bartl.) Dietr.: 444 (1839). Type: Kleinriviersbergen, *Ecklon s.n.* (B†, holo.; S!). Lectotype chosen here: *Ecklon s.n.* [det. Bartl.] (S).

Blaeria barbigeroides sensu Alm & Fries: 235 (1924); Bond & Goldblatt: 239 (1984); Oliver: 145 (1987b).

This very distinct species was referred to as *Blaeria barbigeroides* based only on the assumption that the material fitted the description of Salisbury's *Erica barbigeroides* (1802), there being no extant type specimen. For further details see below under Insufficiently known species.

The new name is an adaptation of the name by which this well-known species of the coastal regions of the Caledon District has been known for many years.

The species is confined to sandy level areas that are often wet in winter in the coastal region of the southwestern Cape from Rooi Els in the west to Sondagskloof (Sandies Glen) near Napier in the east (Figure 1). In this region it may be found from just above the spray zone near the sea up to an altitude of 760 m on the nearby mountains.

* Stellenbosch Herbarium, National Botanical Institute, P.O. Box 471, Stellenbosch 7599.
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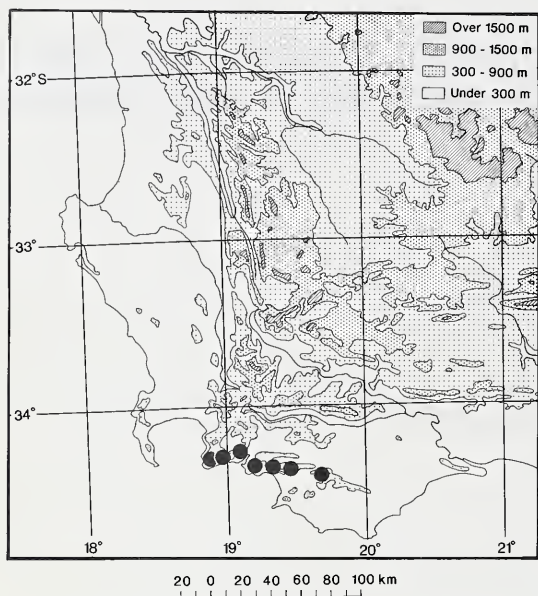


FIGURE 1.—The known distribution of *Erica barbigeroides*.

E. barbigeroides forms sparsely branched, virgate shrublets up to 400 mm tall, is covered with numerous long hairs and has up to 24 flowers grouped together in closely packed heads at ends of branches. Heads often partially pendent. Flowers somewhat sticky due to secretion of viscid matter from sessile glands on margins of sepals.

It is allied to two other species mentioned here, *E. ericoides* and *E. russakiana*, both of which occur in the same area near Hermanus, but never grow together. Both of the latter species form many-branched shrublets and are smaller in all parts of the inflorescence and flower.

Vouchers: Ecklon & Zeyher 260 [loc. 58.8] (BOL, G, MO, S, SAM, W); Ecklon & Zeyher s.n. [loc. 58.8] (K, LD, P, UPS, W, Z); Oliver & Palser 83 (E, MEL, NY, PRE, STE); Schlechter 95II (BM, BOL, G, K, MO, PRE, STE, W, Z). 70 other collections examined.

2. *Erica equisetifolia* Salisb. in Transactions of the Linnean Society 6: 342 (1802). Type: locality & collector unknown, Herb. Salisb. (K, holo.).

Blaeria equisetifolia (Salisb.) G. Don: 805 (1834); Alm & Fries: 239 (1924); Salter: 658 (1950); Bond & Goldblatt: 239 (1984); Oliver: 145 (1987).

B. purpurea L. f.: 122 (1782) nom. illegit. non Berg. (1767) [= *Simonecheilus purpureus* (Berg.) Druce]; Thunb.: 8 (1802); Klotzsch: 221 (1838); N.E. Br.: 323 (1905); Alm & Fries: 239 (1924) pro parte. Type: Thunberg s.n. (UPS, holo.).

B. dumosa Wendl.: t.38 (1808); Roem. & Schult.: 170 (1818); G. Don: 805 (1834); N.E. Br.: 323 (1905), synonym. nov. Type: Wendl.: t.38.

B. dumosa var. *breviflora* N.E. Br.: 323 (1905), synonym. nov. Syntypes: Caledon Div., mountains near Genadendal, Bolus 5419 (BOL!, K!, PRE!) and in Herb. Norm 613 (K!); *ibid.* Guthrie 3140 (?); without locality, Drège s.n. (K!).

B. campanulata Benth.: 698 (1839); N.E. Br.: 324 (1905), synonym. nov. Syntypes: Cape, Drège s.n. (?); Burchell 7693 (K!); Burchell 7773 (K!, P!, W!).

B. flava H. Bol.: 239 (1894); N.E. Br.: 322 (1905), synonym. nov. Syntypes: Zwartberg near Caledon, Jan. 1885, 800 m, Bolus 5147 (BOL!,

K!, PRE!, STE!) & sub Herb. Norm. 611 (BM!, BOL!, G!, NH!, P!, PRE!, SAM!, UPS!, W!).

Erica parvula Guth. & Bol.: 171 (1904), synonym. nov. Type: Stellenbosch Div.; on a rock near the mouth of the Steenbras River, 20–30 ft. above the sea, Guthrie 3710 (BOL, holo.).

Blaeria oppositifolia L. Guthrie: 21 (1928), synonym. nov. Type: Hottentots Holland Mountains, Jan. 1924, Stokoe in BOL 17674 (BOL, holo., K!).

Common and widespread in mountains of southwestern Cape from Cape Peninsula to Bain's Kloof in north to western part of Bredasdorp District in south and occurs from sea level to summits of mountains at 1 600 m (Figure 2). Highly variable species in habit, flower size and shape, anther form and in having some collections with more than usual number of four stamens.

Basic type forms rounded low shrublet with deep pink, narrowly tubular flowers with four dark brown, exserted anthers. In some cases, mainly at lower altitudes, plants can be erect and reach 500 mm in height when growing in old fynbos. Flowers may be short with corolla 2.5 mm long and open campanulate to large with corolla 4 mm long and tubular.

Several species formerly recognised as distinct have been reduced to synonymy under *E. equisetifolia* on the grounds of overlap in characters caused by the variation found in the numerous collections of this complex. *E. equisetifolia* and *Blaeria dumosa* were distinguished on the single character of anther shape, the former having straight-sided anthers whereas the latter had anthers that were obtriangular in outline with a constriction above the decurrent appendages. The straight-sided collections come mostly from the Cape Peninsula and the other material from the inland mountains. There are collections from the mainland which fit equally well in either of the two species.

Salisbury's type is a small branchlet with 'Equisetifolia MS' written in his own hand. It possesses six flowers with only a single stamen remaining. From this stamen it is

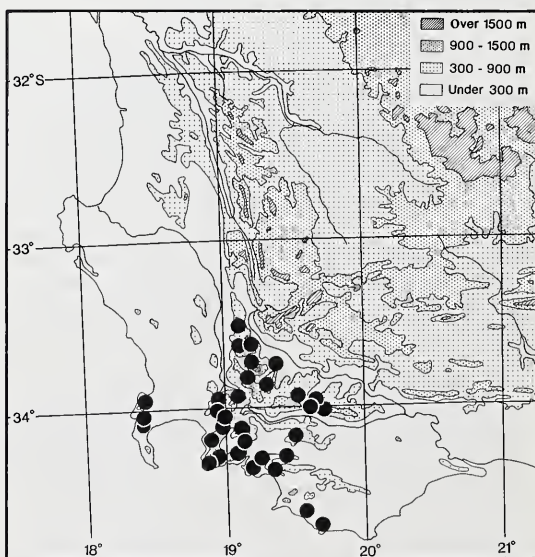


FIGURE 2.—The known distribution of *Erica equisetifolia*.

seen that the anther is the straight-sided form, most probably from the Cape Peninsula, and that there is only one small awn on one side.

Blaeria flava was described by Bolus on the grounds of the yellow colour of the corolla. This would appear to be the only character showing any discontinuity in this complex which has only pink or white flowers. The species is known only from the original collection from the Swartberg at Caledon where no pink- or white-flowered collections have been made. A thorough investigation of the Swartberg may produce more evidence for assigning this material some taxonomic status.

The problem of the similarity between *E. equisetifolia*, *Blaeria campanulata* and *E. parvula* is mentioned (Oliver in press A) as a case for reducing *Blaeria* to synonymy under *Erica*.

B. campanulata was based on material collected from rock ledges on the cool, southeast side of the top of the mountains of Baviaanskloof above Genadendal from where it is known through only a few collections. Plants are small and very compact, the white flowers have exerted dark stamens which range from 5–8 per flower and mostly 3-locular ovaries (Oliver 8978 & 9081). A recent collection (Oliver 8813) with only 8-stamened flowers has been made on the lowest dry northern slopes near McGregor. This material, in turn, was found to be morphologically inseparable from *E. parvula* which is confined to the Elgin/Betty's Bay area near the coast. This latter species also forms compact woody shrublets with white flowers. It grows mostly on rocks in streambeds. Apart from the more variable number of stamens and ovary locules the material of these two species is indistinguishable. There could, however, be some purpose in recognizing the high altitude form from Baviaanskloof as a subspecies. This will need some further investigations and assessment.

Several new species from the Kogelberg and Hermanus areas that are closely allied to this species are being described separately (Oliver 1993). One of these is recorded as producing a putative natural hybrid with *E. equisetifolia*.

An anomalous form with mostly opposite leaves was collected by Stokoe somewhere in the Hottentots-Holland Mountains. Sometimes one can find an occasional 2-nate arrangement of leaves on a branchlet in *E. equisetifolia*, and in other species, such as the *E. tenuifolia* L./*E. lutea* Berg. complex, whole branchlets or even branches can have 2-nate leaves. This condition alone is not regarded as sufficiently distinct to warrant taxonomic recognition, especially as it is known only from a single small collection that cannot be relocated in the field.

Vouchers: Bolus 5420 (BOL, K, LD, NBG, PRE, STE, W); Burchell 7773 (K, P, W); Oliver 8813 (BM, BOL, E, G, MO, MEL, NY, P, PRE, S, STE, UPS, W); Oliver 9081 (E, MEL, PRE, STE); Schlechter 9639 (BM, BOL, E, G, K, MO, P, PRE, STE, W); Schlechter 10265 (BM, E, K, MO, P, PRE, S, STE, W); Schlechter 10339 (BM, G, K, MO, P, PRE, S, W); Sieber 165 (G, G-DC, K, LD, M, MO, P, PRE, S, W). 200 other collections studied.

3. *Erica ericoides* (L.) E.G.H. Oliver, comb. nov.

Blaeria ericoides L., Species plantarum 1: 112 (1753); L.: 331 (1771); Willd.: 629 (1798); Thunb.: 7 (1802); Wendl.: 73 (1808); Ait.: 248 (1810);

Roem. & Schult.: 168 (1818); Bartl.: 649 (1832); Klotzsch: 663 (1833); G. Don: 804 (1834); Klotzsch: 222 (1838); Benth.: 698 (1839); Rach: 788 (1853); N.E. Br.: 325 (1905); Alm & Fries: 233 (1924); Salter: 658 (1950); Bond & Goldblatt: 239 (1984); Oliver: 145 (1987). *E. blaeria* Thunb.: 72 (1794); Thunb.: 358 (1823). *E. dumosa* Salisb.: 296 (1796); Salisb.: 341 (1802). Lectotype: *Hermann s.n.* in Hermann Herbarium vol. 4 fol. 61 (BM, STE, photo!), selected by Oliver (in press B).

Blaeria affinis N.E. Br.: 325 (1905). Type: Caledon Div., mountains near Vogel Gat, near the mouth of the Klein River, 1500 ft., Schlechter 10418 (K, holo.; BM!, BOL!, P!, PRE!).

This species, the type of Linnaeus' genus *Blaeria*, is very common in dry rocky areas on flats or in the mountains from the Cape Peninsula eastwards along the coast to just beyond Stanford (Figure 3). In some areas it forms dominant stands which are very evident due to the strong honeylake scent emitted by the flowers.

E. ericoides is a very distinct species which is often confused with species from some of the minor genera, namely *Sympieza labialis* (Salisb.) Druce, *Simocheilus purpureus* (Berg.) Druce and *Syndesmanthus articulatus* (L.) Klotzsch, all of which have similar looking heads of pale pink tubular flowers with exerted dark brown anthers. The *Erica* can be easily identified by its 4-celled multi-ovuled ovary which produces a dehiscent capsular fruit.

Alm & Fries correctly placed Brown's *B. affinis* in synonymy under this species. The species was based on the smaller flowerheads and finer branches of a single collection from the Hermanus area. The numerous collections of *E. ericoides* show a range of variation which includes this slighter form.

E. ericoides is allied to *E. russakiana* and to a lesser extent *E. barbigeroides* (q.v.).

The typification of *E. ericoides* is being formalised in conjunction with R.F. Barrie (BM) for the programme on the typification of Linnaean taxa (Oliver in press B).

Vouchers: Schlechter 7554 (BM, E, G, K, MO, P, PRE, STE, UPS, W, Z); Schlechter 10401 (BM, BOL, E, G, K, MO, P, PRE, S, STE,

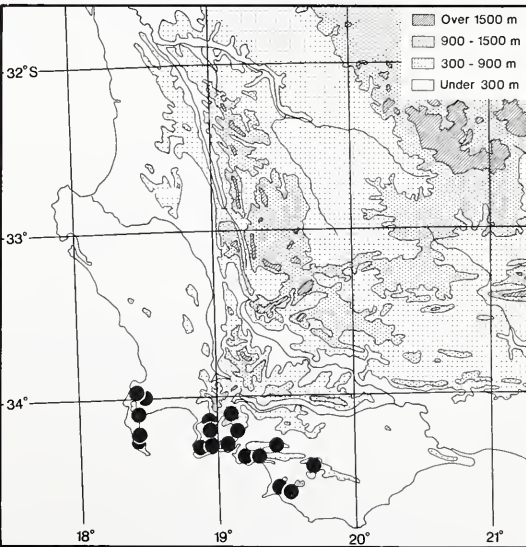


FIGURE 3.—The known distribution of *Erica ericoides*.

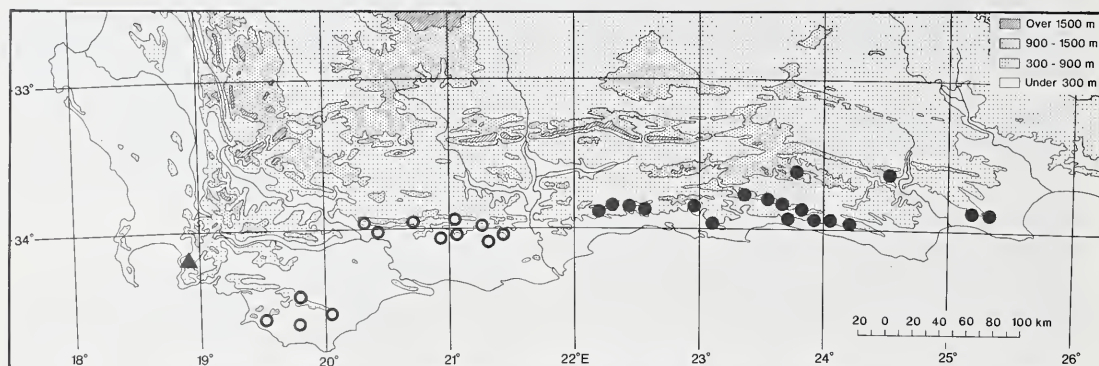


FIGURE 4.—The known distribution of *Erica fuscescens*, ●; *E. klotzschii*, ○; and *E. multiflexuosa*, ▲.

UPS, W); Sieber 172 (G-DC, K, LD, M, MO, P, S, STE, W). 170 other collections examined.

4. *Erica fuscescens* (Klotzsch) E.G.H. Oliver, comb. nov.

Blaeria fuscescens Klotzsch: 657 (1833); Benth.: 697 (1839); N.E. Br.: 321 (1905) pro parte excl. synonym *Erica sagittata* Klotzsch ex Benth.; Alm & Fries: 239 (1924). *Blaeria fuscescens* Dietr.: 443 (1839). Type: Cape of Good Hope, Mundt & Maire s.n. (B†, holo.; El, G!, K!, P!, W!). Lectotype chosen here: Mundt & Maire s.n. [det. Klotzsch] (P!).

This species is common on the southern slopes of the Outeniqua and Tzitzikama Mountains in the southern Cape (Figure 4). It has also been recorded from the Van Stadens Mountains where it is sympatric with the closely related *E. sagittata* (see below), but does not, as far as I am aware, grow together with it. The numerous white flowers with exerted black anthers make this a very striking plant. The plants are bushy and fairly large, up to 1.5 m tall, whereas in *E. sagittata* they are much smaller and sparser with more crowded flowers due to the different inflorescence type.

Vouchers: Burchell 5910 (BOL, K, P, UPS); Fourcade 831 (BOL, K, STE, Z); Galpin 3717 (BOL, K, PRE, SAM); Mundt & Maire s.n. (E, G, K, P, W) [ex B, det. Klotzsch]; Oliver 9250 (PRE, STE). 65 other collections examined.

5. *Erica klotzschii* (Alm & Fries) E.G.H. Oliver, comb. nov.

Blaeria klotzschii Alm & Fries: 237 (1924). Type: Cape of Good Hope Lichtenstein s.n. (B†, holo.; S fragm.). *B. pusilla* Klotzsch: 659 (1833) nom. illegit. non *Blaeria pusilla* L.: 39 (1767) [= *Simocheilus purpureus* (Berg.) Druce], non *Erica pusilla* Thunb.: 70 (1794), non *Erica pusilla* Salisb.: 374 (1802); Benth.: 698 (1839); N.E. Br.: 322 (1905). Lectotype chosen here: Lichtenstein s.n. (S!).

E. klotzschii was rather anomalous in the genus *Blaeria* as it had no close relatives and possessed only a superficial resemblance to *E. longimontana* [= *B. coccinea*]. The flowers are very small and are borne at the ends of most lateral branches on the plant thus producing plants almost completely covered by pale pink to dull cream flowers. The anthers are relatively large, exerted and slightly versatile. This fact coupled with the dull colour of the corolla, the small size of the flower and the far-exserted cyathiform stigma strongly suggest wind pollination in this species. This was substantiated in populations near

Swellendam in which plants gave off clouds of pollen when disturbed early in the morning.

The species occurs on dry shaley hills and slopes at the base of mountains from Elim to Swellendam and eastwards as far as Albertinia often associated with Renosterveld vegetation (Figure 4).

Vouchers: Bolus 8461 (BM, BOL, K, UPS); Oliver 4297 (BM, PRE, STE); Zeyher 3331 (BOL, GRA, K, P, PRE, S, SAM, W, Z). 40 other collections examined.

6. *Erica longimontana* E.G.H. Oliver, nom. nov.

Blaeria coccinea Klotzsch: 657 (1833), non *Erica coccinea* L. (1753); Benth.: 697 (1839); N.E. Br.: 321 (1905); Alm & Fries: 236 (1924). Type: Cape of Good Hope, Mundt & Maire s.n. (B†, holo.; K!—BOL, fragm., S!, W!). Lectotype chosen here: Mundt & Maire s.n. [ex B & det. Klotzsch] (K!).

B. fastigiata Benth.: 697 (1839), non *E. fastigiata* L. (1771); N.E. Br.: 321 (1905). Type: Cape Colony, Burchell 7331 (K, holo.; S!).

This species is common along the southern slopes of the Langeberg from Swellendam to the western Outeniqua Mountains at the Robinson's Pass (Figure 5) where it is often dominant in seepage zones, hence the new name chosen for the species.

Alm & Fries were correct in reducing Bentham's *B. fastigiata* to synonymy. This latter species was separated off on the grounds of having only finely puberulous parts. This form is found in the Swellendam area where it co-exists with the form with longer hairs.

Vouchers: Oliver 9106 (BM, E, K, MEL, MO, NY, P, PRE, STE); Schlechter 2055 (BM, BOL, G, K, PRE, S, UPS). 42 other collections examined.

7. *Erica multiflexuosa* E.G.H. Oliver, nom. nov.

Blaeria flexuosa Benth.: 698 (1839), non *E. flexuosa* Andr. (1798); N.E. Br.: 324 (1905). Type: at Steenbras River, prov. Stellenbosch, Niven s.n. (Herb Lambert; G-DC!). Lectotype chosen here: Niven 6 (Herb. Lambert in K!).

B. purpurea Alm & Fries: 239 (1924) pro parte.

This species is confined to a small area on the lower northern slopes of the Kogelberg complex around the Steenbras Dam (Figure 4) where it grows in open sandy areas between low restiad clumps. It forms low rounded

but sparse shrublets with very intertwined branches which are sparsely leafy. The flowers are a dull cream colour and, hanging downwards, are rather inconspicuous.

E. multiflexuosa belongs to the *E. equisetifolia* complex but can be distinguished by its intertwined branches, its obovoid, dull cream, pendent flowers and included mucous yellow-brown anthers. Like other species of the complex it can have opposite leaves on some branches.

Brown (1905) was somewhat confused about this species because he cited *Niven 6* & *7*, both from the Steenbrass River, under *Blaeria flava* and *Niven 6* also under *Blaeria flexuosa*.

Specimens examined

CAPE.—3418 (Cape Town): Kogelberg Forest Reserve, E foothills of Spinnekopsnes Range, 854 m. (—BB), 2-05-1970, *Boucher 1285* (K, STE); Steenbrass Reservoir valley, (—BB), 14-12-1933, *Galpin 12405* (K, PRE); Steenbrass area, (—BB), 1-05-1948, *Levyns 8879* (BOL); *ibid.*, *Levyns 11533* (BOL); *ibid.*, 7-12-1926, *Middlemost 122* (BOL); *ibid.*, *Niven 6* (G-DC, K—BOL fragm.); *ibid.*, *Niven 7* (K); NE end of Kogelberg range, 450 m. (—BB), 20-03-1983, *Oliver 8824* (PRE, STE); Steenbrass, Wolvern Kloof, (—BB), 28-02-1931, *Stokoe 2563* (BOL, PRE, STE); Steenbrass plateau & vlakte, (—BB), 18-02-1921, *Stokoe 8917* (BOL); *ibid.*, 1931, *Stokoe 8889* (BOL, PRE); near Steenbrass Reservoir, (—BB), 14-12-1933, *Salter 4207* (BM, K, SAM).

8. *Erica russakiana* E.G.H. Oliver, nom. nov.

Blaeria kraussiana Klotzsch ex Walpers: 728 (1843) non *E. kraussiana* Klotzsch ex Walpers: 728 (1843); Klotzsch ex Walpers: 824 (1844); N.E. Br.: 326 (1905); Alm & Fries: 235 (1924); Oliver: 267 (1984). Type: Babylon's Tower, Hemel en Aarde, *Krauss 973* (B†, holo.; BOL!, K!, M!, S!, UPS!, W!, Z!). Lectotype chosen here: *Krauss 973* (K!—BOL fragm.).

Acrostemon concinnus N.E. Br.: 351 (1905). Type: Swartberg, Caledon, *Bodkin sub Bolus 9228* (BOL, holo.; K!).

It is surprising that Brown overlooked the similarity between his species and that of Klotzsch which he included in his revision, especially seeing that his taxon was the only one in *Acrostemon* with a 4-locular ovary.

The species, of which only four collections exist, is confined to the northern slopes of the Klein River Mountains north of Hermanus with one collection from the Swartberg at Caledon (Figure 5). It forms a sparsely branched low compact shrublet up to 300 mm tall which becomes erect and more sparse when very old. The flowers are superficially similar to those of the common

E. ericoides which occurs in the same area but forms a large, woody spreading shrub up to 1.0 × 1.5 m. The other species with similar heads of flowers, *E. barbigeroides*, from the same area but near the southern base of the mountains, forms a sparsely branched erect shrublet with much larger and more numerous flowers per head.

The name chosen above continues to commemorate the original collector, Ferdinand Krauss, but in anagrammatic form.

Specimens examined

CAPE.—3419 (Caledon): Swartberg, Caledon, (—AB), 01-1901, *Bodkin sub Bolus 9228* (BOL, K); Babylon's Tower near Hemel-en-Aarde, 183–244 m, (—AC/AD), 08-1838, *Krauss 973* (BOL, K, M, MO, S, UPS, W, Z); Klein River Mtns above Diepgat, 610 m, (—AD), 1-02-1971, *Oliver 3246* (PRE, STE); *ibid.*, 22-02-1985, *Oliver 8688* (STE).

9. *Erica sagittata* Klotzsch ex Benth. in DC., *Prodrumus* 6: 681 (1839). Type: in Vanstaaden mountains, *Drège s.n.*, (B†, holo. —BOL, sketch). Lectotype chosen here: Vanstaadesberg [Van Stadensberg], 1000 ft., 27-12-1829, *Drège 7725* (P!).

Blaeria sagittata (Klotzsch ex Benth.) Alm & Fries: 238 (1924).

B. grandis N.E. Br.: 320 (1905). Syntypes: Van Stadens Mountains, *Zeyher 718* (K!), *BOL fragm.*!; *ibid.* *West sub MacOwan 3119* (BOL!, PRE!, SAM!).

B. fuscescens sensu N.E. Br.: 320 (1905) quoad specm. *Drège s.n.*

Brown (1905) noted that Bolus had examined the type of *Erica sagittata* in the Berlin Herbarium and had informed him that despite its poor quality 'there can be no doubt of its identity with *Blaeria fuscescens* Klotzsch'. Bolus himself made a sketch of the type and some dissections of the flower and noted in his herbarium that it contained three branches 12–14 inches long on one sheet and only one imperfect flower in a capsule and that the ticket labelled it as *Drège 7725* from Van Stadensberg. Bentham noted the type as 'defloratum cum fl. unico delapso'. If the specimen had possessed more flowers Bolus would have seen that the axillary inflorescence on an absolute brachyblast differed from the terminal 3-flowered inflorescence on a leafy lateral branchlet in *Blaeria fuscescens* and that the two species cannot be confused.

The rather sparse material of *Drège 7725* in Paris, consisting of five young plants with two flowers in place on

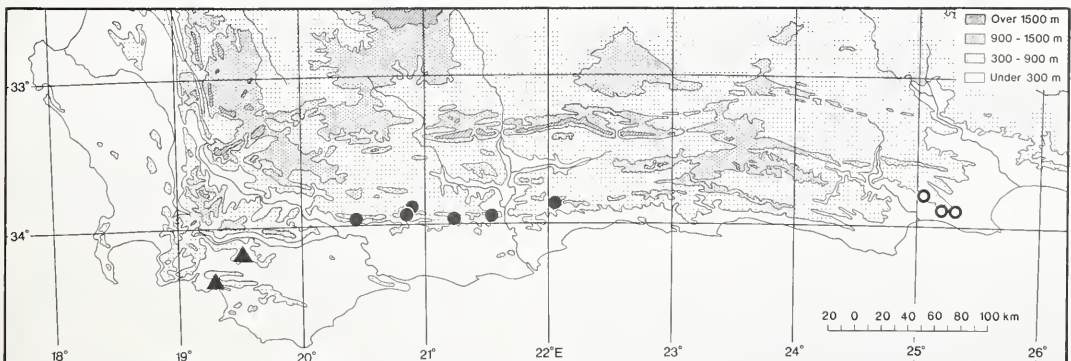


FIGURE 5.—The known distribution of *Erica longimontana*, ●; *E. russakiana*, ▲; and *E. sagittata*, ○.

one plant, clearly matches the sketches of Bolus. It is undoubtedly from the same collection as the lost Berlin material.

This species is very localized in the Van Stadens Mountains west of Port Elizabeth (Figure 5) where it is sympatric with *E. fuscescens*. *E. sagittata* can be distinguished from the latter species on a number of characters. Apart from the type of inflorescence mentioned above, it has larger flowers with corolla 6 mm long, not less than 4 mm, leaves open-backed and 1–2 mm broad, not sulcate and 0.5–1.0 mm long, and branches glabrous and distinctly ridged, not puberulous and rounded.

E. sagittata is remarkable in being very similar to *Erica carnea* L. from Europe which also has flowers borne on absolute brachyblasts and exerted dark stamens. The two species could easily be mistaken for one another if the origin of the material were not known. This is undoubtedly a case of convergent evolution.

Specimens examined

CAPE.—3324 (Steytlerville): Elandsrivierberg area in Otterford Forest Reserve, 762 m, (—DB), 9-09-1973, *Oliver 4455* (MO, PRE, STE), 3325 (Port Elizabeth): Blueberg, Loerie Plantation, 22-09-1934, (—CC), *Dix 31* (BOL, GRA, K, PRE, STE); Van Stadens Gorge, Witteklip, (—CC), 09-1981, *Muller s.n.* (STE); Van Stadens Mtns, 305 m, (—CC/CD), 27-12-1829, *Drège 7725* (P); *ibid.*, 09-1909, *West 477* (BOL, SAM); *ibid.*, *West sub MacOwan 3119* (BOL PRE); *ibid.*, *West sub MacOwan 3111* (BOL); *ibid.*, *Zeyher 718* (BOL, K); *ibid.*, *Zeyher 3266* (SAM).

INSUFFICIENTLY KNOWN SPECIES

Blaeria barbiger (Salisb.) G. Don: 805 (1834). Type: Hottentots Holland, *Masson s.n.* (?).

Erica barbiger Salisb.: 341 (1802).

Salisbury's type does not appear to exist, as no specimen referable to this species collected either by Masson or labelled as 'Herb. Salisb.' nor one determined by Salisbury, has been found in Kew or the British Museum, where all the types of Salisbury's species of Cape Ericaceae are known to be housed. Salisbury's description is insufficient to be of use to ascertain the true identity of his species. No mention was made of either the distinct capitate heads of flowers (10–24) or of the glandular nature of the leaves and calyx. His description could refer to a number of species in *Blaeria* or even some other genera in the subfamily. Without an authentic specimen it is not possible to tie down Salisbury's concept '*Erica barbiger*'.

Bentham (1839) referred Salisbury's species to *Blaeria revoluta* Bartl. without having seen a type since he did not cite a Masson collection. This was taken up by most subsequent authors with Brown citing the synonymy as 'sec. Benth.'.

EXCLUDED SPECIES

With the description of numerous species under the genus *Blaeria* during the late 1700's and early 1800's there are many combinations under *Blaeria* which are no longer in use for species removed to other genera. A full list of these is given by Alm & Fries (1924: 262, 263) based on

the taxonomy of the family in *Flora capensis* (Brown 1905). With a revision of the family in southern Africa currently in progress, many changes to the taxonomy and therefore nomenclature, will be necessary. For this reason a listing of all the excluded species is not published at this stage as new combinations would have to be created of which many would soon be redundant.

However, one species not covered by the listing of Alm & Fries is: *Blaeria muirii* L. Guthrie: 179 (1924) = *Thoracosperma galpinii* N.E. Br.: 330 (1905).

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Studies in the Ericoideae (Ericaceae). XIII. Three new species of *Erica* from the southwestern Cape

E.G.H. OLIVER*

Keywords: Cape Province, *Erica*, Ericoideae, new species, taxonomy

ABSTRACT

With the recent inclusion of the genus *Blaeria* under *Erica*, three new species, formerly regarded as 'incertae' in that genus, are now described: *Erica chiroptera* E.G.H. Oliver from the Kogelberg Reserve, *Erica hermani* E.G.H. Oliver and *Erica ioniana* E.G.H. Oliver, both highly localised endemics from Hermanus.

UITTREKSEL

Met die onlangse insluiting van die genus *Blaeria* by *Erica*, word drie nuwe spesies wat voorheen onder die 'incertae' van daardie genus behoort het, nou beskryf: *Erica chiroptera* E.G.H. Oliver van die Kogelberg Reservaat, *Erica hermani* E.G.H. Oliver en *Erica ioniana* E.G.H. Oliver, albei uitsers beperkte endemiese spesies van Hermanus.

INTRODUCTION

The genus *Blaeria* L. was recognised for over two centuries as separate from *Erica* L. based on the single character difference of four as opposed to eight stamens in the latter. In a recent paper (Oliver in press) it is shown that there is an overlap between the two genera and that there is a clear case for regarding *Blaeria* as polyphyletic. As a result the genus *Blaeria* is being reduced to synonymy under *Erica* (Oliver 1993).

Material which had been placed in the 'incertae' under *Blaeria* and which clearly constituted several new taxa, has remained undescribed because of the problem with the delimitation of *Blaeria*. These taxa are now described in this paper.

Erica chiroptera E.G.H. Oliver, sp. nov. in genere distincta propter antheras quatuor inclusas latissimas dorsiventraliter complanatas, capite aliquorum vespertilionum (Chiropteridae) similes, flores albos ad roseos; affinitate *E. equisetifoliae* Salisb. sed facie antherarum exsertarum differt.

Fruticulus erectus ad 500 mm altus. Rami erecti vel flexuosi glabri trigoni, cortice griseo. Folia 3-nata, 1.5–3.5 × 0.5–1.0 mm, erecta appressa, angusta, sulcata glabra ciliata vel eciliata, breve petiolata. Flores 3–6[9] ad extremis ramorum et ramulorum lateralium; pedicellus 1.5–3.0 mm longus glaber; bractea submediana 0.5–1.3 mm longa lineari-oblonga glabra ciliata; bracteolae bractearum similes minores. Calyx 4-lobatus, cyathiformis 0.8–1.5 mm longus, glaber; lobi deltoidei, sulcati, sparse ciliati pilis parvis et glandibus sessilibus. Corolla 4-lobata 2.7–3.6 × 2.0–2.4 mm quadrangularis cyathiformis base porcis calyce alternantibus glabra pustulato-rugosa; lobi late rotundati irregulariter crenulati ad subfimbriati. Stamina 4 inclusa; filamenta 0.9–1.6 mm longa recta glabra; anthera 0.9–1.4 × 0.8–1.4 mm erecta terminalia

late obcuneata dorsiventraliter complanata marginibus strigulosis, thecis patentibus poro rotundato $\frac{1}{4}$ longitudine thecae appendiculatis, cristis late obcuneatis decurrentibus. Ovarium 4-loculare 0.7–1.0 × 0.7–1.0 mm distincte quadrangulare late ellipsoideum ad obovoideum glabrum, nectario reducto vel absenti, ovulis 2 in quoque loculo, ex placenta apicali pendulis, lateraliter compressis; stylus exsertus 2.0–2.5 mm longus teres base expansus glaber; stigma simplex. Fructus late ellipsoideus ad obovoideus, septis longitudine $\frac{2}{3}$ connatis, valvis ellipsoideis, 1.5 × 1.2 mm, obtusis; semina ellipsoidea, subreticulata. Figura 1.

TYPE. — 3418 (Simonstown): Cape, Caledon District, Kogelberg Forest Reserve, neck at head of the Rooi Els valley near Wynand Louwsbos, 366 m, (–BD), 11 November 1970, Oliver 3097 (STE, holo.; BM, BOL, E, K, MEL, MO, NY, P, PRE, S, isotypes).

Erect, open or compact shrublet up to 500 mm tall. Branches erect or wiry and flexuose, glabrous, with slight infrafoliar ridges and trigonous when young, bark grey flaking irregularly or mainly below leaves, becoming red-brown. Leaves 3-nate, erect and appressed, subimbricate, narrowly ovate to narrowly elliptic to linear-elliptic, 1.5–3.5 × 0.5–1.0 mm, subobtuse to acute, markedly convex abaxially, flat or slightly concave adaxially, sulcate, glabrous, with or without short fine cilia and marginal sessile glands, strigulose at apex; petiole 0.3–0.5 mm long, glabrous. Flowers 3–6[9] at ends of main and short subterminal lateral branchlets or brachyblasts, pendent; pedicel 1.5–3.0 mm long, terete, glabrous, red; bract submedian, linear-oblong, 0.5–1.3 mm long, glabrous, ciliate, sometimes with marginal sessile glands also, lower bracts in an inflorescence larger and sometimes sulcate, others not sulcate; bracteoles 2 just above bract and like bract, 0.3–0.7 mm long. Calyx 4-lobed to half its length, cyathiform, 0.8–1.5 mm long, glabrous; lobes narrowly to broadly deltoid, clasping base of corolla, sulcate in upper half, green, sparsely ciliate with short hairs and sessile glands. Corolla 4-lobed, quadrangular cyathiform, 2.7–3.6 × 2.0–2.4 mm, dirty white to very pale pink, 4-ridged at base with ridges alternating with calyx lobes,

* Stellenbosch Herbarium, National Botanical Institute, P.O. Box 471, Stellenbosch 7599.
MS. received: 1992-06-09.

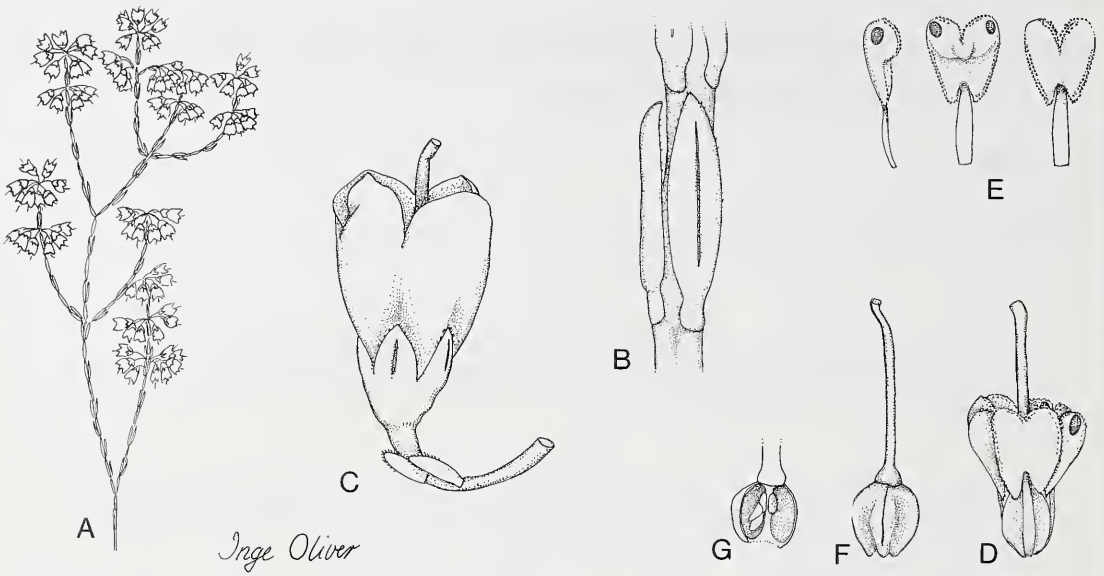


FIGURE 1.—*Erica chiroptera*: A, flowering branch, $\times 2$; B, close-up of branch with leaves; C, flower; D, androecium; E, anther, side, front and back views; F, gynoecium; G, ovary, longitudinal section; B–G, $\times 25$. All drawn from the type, *Oliver 3097* (STE).

glabrous, pustulate-rugose; lobes erect to slightly spreading, broadly rounded, $\frac{1}{4}$ the length of corolla, irregularly crenulate to subfimbriate. *Stamens* 4 included; filaments 0.9–1.6 mm long, straight, erect, slightly broadening downwards, glabrous; anthers erect, placed just above ovary, terminal, broadly obcuneate, with appendages 0.9–1.4 \times 0.8–1.4 mm, dorsiventrally flattened, strigulose on edges; thecae spreading in a broadly V-shaped arrangement, 0.5–0.9 mm long; pore rounded, $\frac{1}{4}$ the length of theca; appendages broadly obcuneate, decurrent for just more than half their length. *Ovary* 4-locular, distinctly quadrangular, broadly ellipsoid to obovoid, 0.7–1.0 \times 0.7–1.0 mm, glabrous, nectaries very reduced or absent, septa joined for half their length from base; ovules 2 per locule, pendulous one above other from apical placenta, laterally compressed; style exserted, 2.0–2.5 mm long, terete, enlarging slightly below stigma, occasionally bent at apex, with enlarged basal portion forming a cap on ovary apex, glabrous; stigma simple. *Fruit* broadly ellipsoid to obovoid, septa joined for $\frac{2}{3}$ of their length, valves broadly elliptic, obtuse, 1.5 \times 1.2 mm; seeds ellipsoid, light brown, subreticulate. Figure 1.

E. chiroptera is a very distinct species on account of its very broad, dorsiventrally flattened anthers which are reminiscent of the heads of some bats (Order Chiroptera), hence the name. It is, however, related to the extremely variable species complex which is now referred to as *E. equisetifolia* (Oliver 1993) and which occurs in the same region. This latter species forms smaller, more compact rounded shrublets which can, however, become taller and erect when old. Its flowers are pink in colour, sometimes deeply so, and have exserted anthers which are narrow and elongate with small awns.

The species is confined to the Kogelberg Reserve between Grabouw and Betty's Bay (Figure 2) where it grows in sandy quartzitic ground with short restiads.

Specimens examined

CAPE.—3418 (Simonstown): Kogelberg Reserve, lower slopes south of Klein Palmiet River, southwest of Somersfontein, 244 m, (–BB), 27-01-1987, *Oliver 8999* (BM, BOL, G, K, NY, PRE, STE, W); Palmiet River near Elgin, (–BB), 12-1941, *Stokoe 6247 sub SAM 55121* (NGB, PRE, SAM); Kogelberg Reserve, Somersfontein boundary, 275 m, (–BD), 19-11-1969, *Boucher 874* (PRE, STE); Kogelberg Reserve, Louws River road, 335 m, (–BD), 11-03-1970, *Boucher 1179* (PRE, STE); Betty's Bay, plateau behind Cascades, 450 m, (–BD), 10-02-1956, *Levyns 10456* (BOL); Kogelberg Reserve, head of Rooi Els valley near Wynand

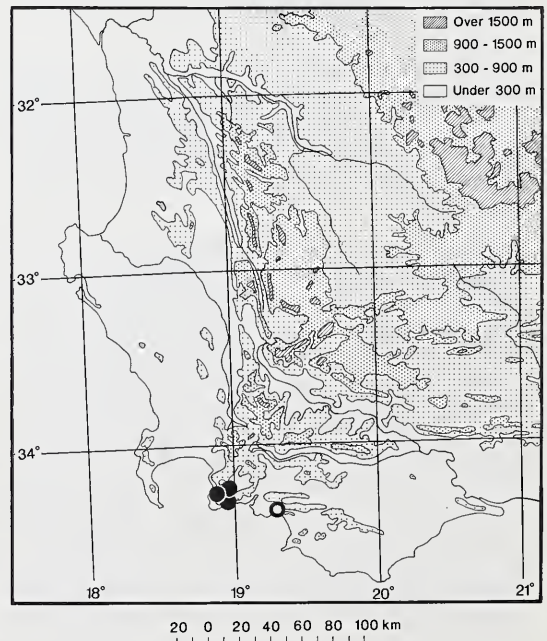


FIGURE 2.—Known distribution of *Erica chiroptera*, ●; and *E. hermani*, ○.

Louwsbos, 366 m, (—BD), 11-03-1970, *Oliver 3097* (BM, BOL, E, K, MEL, MO, NY, P, PRE, S, STE). 3419 (Caledon): Arieskraal, (—AA), 30-12-1944, *Leighton 9/5* (BOL); near Elgin, between Grabouw and the Paardeberg, (—AA), 12-1947, *Stokoe sub SAM 62387* (NBG).

***Erica hermani* E.G.H. Oliver, sp. nov.** ex planitie oraria Hermani, distincta propter folia sessilia appressa, flores roseos campanulatos, stamina 8, antheras atras strigosas exsertas mox deciduas; affinitate *E. equisetifoliae* Salisb. ex eodem loco sed floribus tubulosis, staminibus 4 rare 5–8 (alteris locis) fuscis ad fulvis non deciduis differt.

Fruticulus erectus ad 500 mm altus. Rami erecti, trigoni, infra folia porcati, glabri roseo-brunnescentes, rami veteres cortice frustris griseis. Folia 3-nata sessilia, appressa subimbricata, 1.5–2.8 mm longa, elliptica ad oblongo-elliptica, acuta, glabra apice sparse strigulosa glandibus sessilibus marginalibus. Flores 3–9-nati terminales pendentes; pedicellus 2.0–2.8 mm longus, teretus, glaber; bractea mediana, 0.7–1.0 mm longa, naviculata, glabra esulcata, breve ciliata pilis vel glandis sessilibus; bracteolae subapproximatae bractee similes sed breviores. Calyx 4-lobatus, obconicus ad cyathiformis, 1.2–1.4 mm longus, $\frac{1}{4}$ – $\frac{1}{3}$ connatus, base emarginatus; lobi ovato-deltoidi ad late deltoidei, longe sulcati, ciliati glandis sessilibus atrosanguineis. Corolla 4-lobata 2.4–3.5 × 2.5–3.0 mm, obconica ad campanulata, interdum late campanulata et parum quadrangularis, pustulata, pallido- ad atrosea; lobi longitudine $\frac{1}{4}$ – $\frac{1}{3}$ corollae partes aequantes, late deltoidei et obtusi, erecti ad plus minusve patentes, irregulariter crenato-fimbriati. Stamina 8 exserta; filamenta linearia ± 3 mm longa, sub anthera angustiora, glabra; antherae bene exsertae, prope base dorsaliter affixae, post anthesin mox deciduae, thecis 1.3–1.5 mm longis, erectis, appressis, suboblongo-ovatis, apice prognathis, obtusis,

marginibus strigosis ad base barbatis, nigris. Ovarium 4-loculare 0.6–0.8 × 0.6–0.8 mm, quadrangulare, late ellipsoideum, glabrum, base nectariis parvis; ovula 7–8 in quoque loculo, ex placenta apicali pendentes; stylus exsertus, ± 5.4 mm longus, anguste cylindraceus basaliter amplificatus, glaber; stigma obconica. Fructus late ellipsoideus, septis longitudine $\frac{2}{3}$ connatis, valvis 1.2 × 1.0 mm, late ellipsoideis, truncatis ad emarginatis; semina complanata ellipsoidea, subreticulata, hepatica. Figura 3.

TYPE.—3419 (Caledon): Cape, Hermanus, Fernkloof, sandy lower slopes, 45 m, (—AD), 18 February 1984, *Oliver 8412* (STE, holo.; BM, BOL, E, G, K, MEL, MO, NY, P, PRE, S, W, isotypes).

Sparse, erect shrub to 500 mm tall. Branches very fine, erect, mostly leafy, trigonous when young with infrafoliar ridges, glabrous, becoming round and reddish brown when old with grey infrafoliar flakes of bark. Leaves 3-nate, sessile, appressed, subimbricate, 1.5–2.8 mm long, elliptic to oblong-elliptic, acute, glabrous, sparsely strigulose at apex, with a few sessile marginal glands when young. Flowers 3–9-nate at ends of branches, pendent; pedicel 2.0–2.8 mm long, terete, glabrous; bract median, 0.7–1.0 mm long, naviculate, glabrous, without sulca, shortly ciliate with hairs and/or sessile glands; bracteoles subapproximate, like bract but slightly shorter. Calyx 4-lobed, obconical to cyathiform, 1.2–1.4 mm long, joined for $\frac{1}{3}$ – $\frac{1}{2}$ its length, emarginate at base, green to reddish, lobes ovate-deltoid to broadly deltoid, long sulcate, edged with sessile dark red glands. Corolla 4-lobed, 2.4–3.5 × 2.5–3.0 mm, obconical to campanulate sometimes broadly so and somewhat quadrangular, pustulate, light to dark cerise-pink; lobes $\frac{1}{4}$ – $\frac{1}{3}$ the length of corolla, broadly deltoid and obtuse, erect to slightly spreading, irregularly crenate-fimbriate. Stamens 8 exserted; filaments linear,

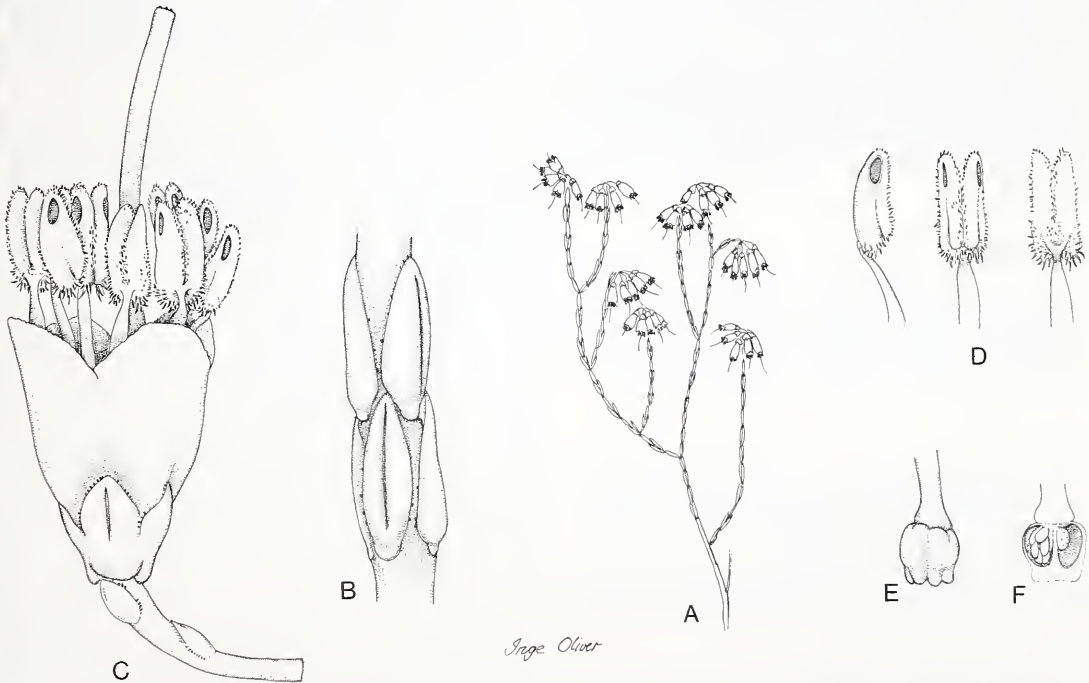


FIGURE 3.—*Erica hermani*: A, flowering branch, × 2; B, close-up of branch with leaves; C, flower; D, anther, side front and back views; E, ovary; F, ovary, longitudinal section; B–F, × 25. All drawn from the type, *Oliver 8412* (STE).

± 3 mm long, narrowed below anther, glabrous; anthers well exerted, dorsally attached near base and soon deciduous after anthesis, thecae 1.3–1.5 mm long, erect, appressed, suboblong-ovate, bent forwards at apex, obtuse, strigose edged to bearded at base, black. *Ovary* 4-locular, $0.6-0.8 \times 0.6-0.8$ mm, quadrangular, broadly ellipsoid, glabrous, with very small nectaries at base; ovules 7–8 per locule, pendent from an apical placenta; style exerted, ± 5.4 mm long, narrowly cylindrical with enlarged base forming a cap to ovary, glabrous; stigma obconical. *Fruit* broadly ellipsoid, septa joined for $\frac{2}{3}$ their length, valves 1.2×1.0 mm, broadly elliptic, obtuse to emarginate; seeds flattened ellipsoid, subreticulate, brown. Figure 3.

Erica hermani is allied to the variable and widespread *E. equisetifolia*, formerly *Blaeria equisetifolia* (Salisb.) G. Don and now including *Blaeria dumosa* Wendl. (Oliver 1993). It differs in having constantly eight stamens with black, strigose, mucous anthers which are shed very soon after anthesis; the flowers are also open-campanulate as opposed to tubular. The shedding of the anthers leaves the black-tipped filaments clearly visible in the mouth of the corolla. The anthers of *E. equisetifolia* are variable in shape being mostly long and narrow with decurrent awns in the plants from the Hermanus area. Plants from the inland mountains, formerly referred to *Blaeria campanulata* Benth. and now placed under *E. equisetifolia* (Oliver 1993), have rather similar anthers to *E. hermani* but with decurrent awns.

This species is very restricted, occurring only on the sandy coastal flats near the entrance to the Fernkloof Nature Reserve at Hermanus, hence the specific epithet, (Figure 2) where it is locally common in remnant patches of fynbos. There it co-exists with plants of *E. equisetifolia* which looks remarkably similar, but is easily distinguished on close examination of the flowers.

In the population of the above two species a few plants with slightly different looking flowers were noted and on close examination were found to be intermediates between the two. The possession of nonviable pollen strongly suggested a hybrid origin for these plants.

Specimens examined

E. hermani

CAPE.—3419 (Caledon): Hermanus, Fernkloof, (—AD), 05-1986, *Drewe s.n.* (STE); *ibid.*, 45 m, 18-02-1984, *Oliver 8412* (BM, BOL, E, G, K, MEL, MO, NY, P, PRE, S, STE, W); *ibid.*, 300 m, 12-01-1981, *Williams 3109* (BOL, PRE, STE); Mossel River flats, (—AD), *Williams sub Baker 3043* (STE).

E. equisetifolia [= *Blaeria equisetifolia* (Salisb.) G. Don]

CAPE.—3419 (Caledon): Hermanus, sandy lower slopes at Fernkloof, 45 m, (—AD), 18-02-1984, *Oliver 4111* (K, MEL, MO, NY, PRE, STE).

E. hermani \times *E. equisetifolia*

CAPE.—3419 (Caledon): Hermanus, sandy lower slopes at Fernkloof, 45 m, (—AD), 18-02-1984, *Oliver 8413* (PRE, STE).

Erica ioniana E.G.H. Oliver, sp. nov. ex montibus Hermani in genere distincta propter habitum parvum compactum, flores campanulatos cremeos viscidos in capitibus

pendulis occultos, stamina straminea 4 interdum 5; affinitatibus *E. ericoidis* (L.) E.G.H. Oliver et *E. russakianae* E.G.H. Oliver sed inflorescentibus erectis, floribus roseis non viscidis, staminibus fuscis.

Fruticulus compactus ad 150 mm altus. *Rami* glabri vel sparse pubescentes ad villosi, sterigmatis infrafoliaceis, rami veteres irregulariter porcati cicatricibus griseis. *Folia* 4-nata, 3.5–5.0 mm longa oblongo-elliptica sparse villosa, breviter glandulociliata; petiolus appressus, 1.2–1.5 mm longus, ciliatus pilis longis et glandibus sanguineis subsessilibus. *Flores* 12–20 capitibus compactis ad extremis ramorum, dependentes, sub planta occultae; pedicellus 1.3–1.7 mm longus, sparse villosus; bractea subapproximate 1.8–2.5 mm longa, linearis ad lineari-spathulata, foliacea in dimidio superno sulcata, sparse villosa, glandulis sessilibus vel subsessilibus ciliata; bracteolae approximatae, 1.3–2.0 mm longae, lineares ad filiformes aliter bracteae similes. *Calyx* 4-lobatus, 1.4–1.8 mm longus; lobi subliberi anguste oblongo-lanceolati sparse villosi glandulis subsessilibus sanguineis in marginibus et in pagina adaxiali apicem versus, sulcatus. *Corolla* 4-lobata, 2.5 mm longa, campanulata quadrangularis, glabra, viscida, cretacea ad rosea; lobi 1 mm longi expansi ad recurvi. *Stamina* 4(5); filamenta 3 mm longa, linearia, apice latiore flexa; antherae inclusae ad submanifestae, bipartitae, thecis 0.8 mm longis subellipsoideis, glabris, super ovario impendentibus; porum longitudine $\frac{1}{3}$ thecae partes aequans; pollen in tetradis. *Ovarium* 4-loculare, 0.6×0.6 mm, late ovoideum, 4-lobatum, plus minusve emarginatum, glabrum, base nectariis grandibus; stylus 2 mm longus, exsertus; stigma simplex. *Fructus* globosus vel late ovoideus, valvis $1.0 \times 0.8-1.0$ mm late ellipticis, obtusis ad emarginatis; semina ovoideo-ellipsoidea, reticulata, fusca. Figura 4.

TYPE.—3319 (Caledon): Cape, Hermanus, Mossel Neck at SW end of Vogelgat Nature Reserve, 490 m, (—AD), 22 February 1985, *Oliver 8684* (STE, holo.; BOL, K, MO, PRE isotypes).

Low compact shrublet to 150 mm tall with slightly spreading branches. *Branches* glabrous or sparsely pubescent to villous when young, with slight infrafoliar ridges when young, bark with slight infrafoliar flakes otherwise flaking irregularly when old. *Leaves* 4-nate, 3.5–5.0 \times 3.0 mm long, oblong-elliptic, sparsely villous all over and sometimes shortly gland-ciliate, becoming strigose; petiole appressed, 1.2–1.5 mm long, ciliate with long hairs and red subsessile glands. *Flowers* 12–20 in compact heads at ends of branches, facing downwards, hidden under plants and not visible; pedicel 1.3–1.7 mm long, sparsely villous, red; bract subapproximate, 1.8–2.5 mm long, shorter than calyx, linear to linear-spathulate, foliaceous and sulcate in upper half, sparsely villous, edged with sessile to subsessile red glands; bracteoles approximate, 1.3–2.0 mm long, shorter than calyx, linear to filiform, otherwise similar to bract. *Calyx* 4-lobed, 1.4–1.8 mm long; lobes almost free, narrowly oblong-lanceolate, just shorter than corolla tube, sparsely villous, with subsessile red glands on edges and adaxially towards apex, sulcate, hairy, green turning red. *Corolla* 4-lobed, 2.5 mm long, campanulate, 4-angled, glabrous, viscid, cream to pale pink; lobes 1 mm long, spreading to recurved. *Stamens* 4(5); filaments 3 mm long, linear with a broader bent apex; anthers included to just manifest, bipartite, pale yellow

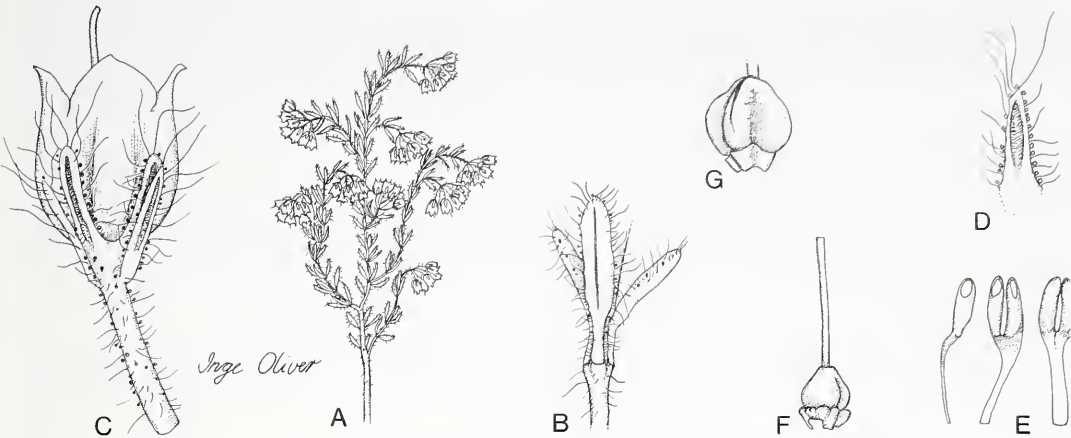


FIGURE 4.—*Erica ioniana*: A, flowering branch, $\times 2$; B, whorl of leaves; C, flower; D, sepal; E, anther, side front and back views; F, gynoeceium; G, mature ovary; B–G, $\times 25$. All drawn from the type, *Oliver 8684* (STE).

brown; thecae 0.8 mm long, slightly ellipsoid, glabrous, bent forwards over ovary; pore $\frac{1}{3}$ the length of theca; pollen in tetrads. *Ovary* 4-locular, 0.6 \times 0.6 mm, broadly ovoid, 4-lobed, slightly emarginate, glabrous, with well-developed nectaries at base; style 2 mm long, exserted; stigma simple. *Fruit* globose or broadly ovoid, valves 1.0 \times 0.8–1.0 mm, broadly elliptic, obtuse to emarginate; seeds ovoid-ellipsoid, reticulate, dark brown. Figure 4.

This distinct species was brought to my attention by Dr Ion Williams of Hermanus (after whom the species is named) who is undertaking surveys of his Vogelgat Reserve in the Klein River Mountains above Hermanus. He assumed the plant to be, from the description, *Blaeria affinis* N.E. Br. which is known only from the type collection made in Vogelgat by Schlechter. This latter

species was reduced to synonymy under *E. ericoides* (L.) E.G.H. Oliver (= *B. ericoides* L.) by Alm & Fries (1924). I have found that Schlechter's collection is just a depauperate form of the common species.

A visit to the area revealed that Williams' populations were a distinct new species with an unusual habit. The plants are low, compact and rounded with the flowers arranged in pendent heads such that they are not easily noticeable when the plants are in full bloom. The pale colour of the corolla and the long hairs of the calyces in the heads of flowers also help to make the flowers less visible. In these respects the species is unlike any other in the area. The other species there with capitate inflorescences, namely *E. ericoides*, *E. russakiana* and *E. barbigeroides* E.G.H. Oliver, have the branches spreading or erect and different, dark brown, basally winged or appendiculate, exserted anthers. The anthers in *E. ioniana* are pale yellowish brown, mucous, included and are narrowed in at the base. They are very similar to those found in *E. multiflexuosa* E.G.H. Oliver, a restricted endemic near Steenbras Dam.

The species is restricted to level sandy places in and near the Vogelgat Reserve, Hermanus, (Figure 5) where three populations have so far been found. The unusual habit strongly suggests some form of pollination by creeping insects with the flowers facing downwards only a short distance from the ground.

Specimens examined

CAPE.—3419 (Caledon): Hermanus, Mossel Neck in Vogelgat Reserve, 490 m, (–AD), 22-02-1985, *Oliver 8684* (BOL, K, MO, PRE, STE); *ibid.*, 480 m, (–AD), 9-02-1985, *Williams 3580* (NBG, PRE); Caledon District, north side of Klein River Mtns above Diepgat, 594 m, (–AD), 22-02-1985, *Oliver 8688* (BM, E, K, MEL, NY, PRE, STE); Hermanus, Fernkloof, Mt Pustulata, 610 m, (–AD), 26-02-1984, *Williams 3531* (HER, NBG, PRE, P, S).

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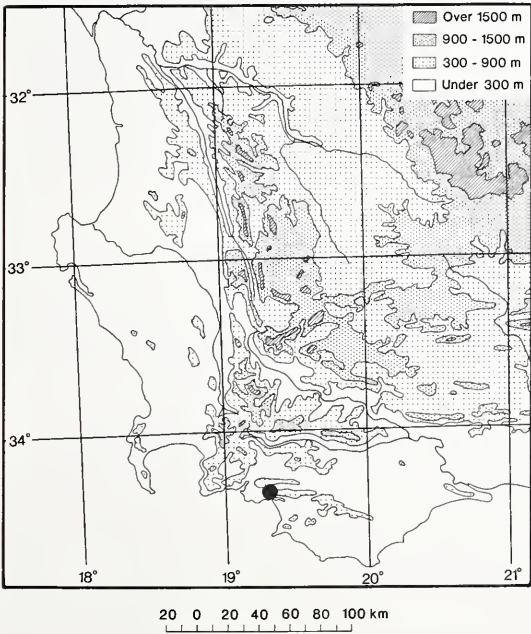


FIGURE 5.—Known distribution of *Erica ioniana*.

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- OLIVER, E.G.H. 1993. Studies in the Ericoideae (Ericaceae). XII. The

placing of the genus *Blaeria* into synonymy under *Erica*; nomenclatural changes for the southern African region. *Bothalia* 23: 1-7.

The hepatics, *Symphyogyna podophylla* and *Pallavicinia lyellii* (Pallaviciniaceae) in southern Africa

S.M. PEROLD*

Keywords: Hepaticae, Pallaviciniaceae, *Pallavicinia lyellii*, southern Africa, *Symphyogyna podophylla*, systematics

ABSTRACT

A detailed description of *Symphyogyna podophylla*, illustrated with photographs of the thalli and spores, is presented. It is compared to *S. hymenophyllum*, with which it may be conspecific. The subcosmopolitan *Pallavicinia lyellii*, also occurring in southern Africa, is described and illustrated with photographs.

UITTREKSEL

'n Uitvoerige beskrywing van *Symphyogyna podophylla*, geïllustreer met foto's van die tallusse en spore, word gegee. Dit word vergelyk met *S. hymenophyllum* waaraan dit gelyksoortig mag wees. Die subkosmopolitiese *Pallavicinia lyellii*, wat ook in suidelike Afrika voorkom, word beskryf en met foto's geïllustreer.

INTRODUCTION

Symphyogyna podophylla is locally quite widespread but of rarer occurrence in southern Africa than *S. brasiliensis*, the other species recorded for the region. The latter was recently redescribed and illustrated with photographs (Perold 1992) in order to draw attention to its southern African synonyms *Pallavicinia capensis*, *Symphyogyna valida* and *S. lehmanniana* (Grolle 1980). Sporulating material of *S. podophylla* held at PRE is rare, *Koekemoer 991* (which was recently collected), being only the fourth specimen of this species which has spores.

Arnell (1963), Vanden Berghen (1965), Grolle (1979) and Grolle & Piippo (1986) regard *S. hymenophyllum* (Hook.) Nees & Mont. as conspecific with *S. podophylla*, but this has been questioned, since there appear to be some differences in the spore ornamentation, as seen on SEM micrographs and in the chemistry of plants from New Zealand (E.O. Campbell pers. comm.). This description of *S. podophylla*, illustrated with photographs, is given in the hope that it may help to answer the question whether *S. hymenophyllum* is conspecific with *S. podophylla* or not.

The subcosmopolitan *Pallavicinia lyellii* of the same family Pallaviciniaceae Migula, but different subfamily Pallavicinioideae (Migula) Grolle, is also redescribed and illustrated with photographs. Differences between the genera *Symphyogyna* and *Pallavicinia* are briefly discussed in Perold (1992) and under *Pallavicinia lyellii* below.

***Symphyogyna podophylla* (Thunb.) Mont. & Nees** in Gottsche, Lindenberg & Nees, Synopsis hepaticarum: 481 (1846); Arnell: 107 (1963); Vanden Berghen: 157 (1965). Type: Cape, 'Promontorium Bonae Spei', leg. Thunberg (25945 UPS, holo.; S, STR, W, iso.).

Jungermannia podophylla Thunb.: 174 (1800); Thunb.: 738 (1823).

S. rigida Steph.: 112 (1914); Steph.: 69 (1917). Syntypes: Rwanda, Rugege-Wald: ca. 1 900 m, leg. Mecklenburg 842; Vulkan-gebiet: Ninagongo ca. 3 500 m, leg. Mecklenburg 2012 (?G). [Syn. fide Vanden Berghen: 159 (1965)].

S. rhizobola (Schwaegr.) Nees & Mont.: 68 (1836). *Jungermannia rhizobola* Schwaegr.: 31 (1814). Type: Réunion (W, iso.). [Syn. fide Grolle: 267 (1979)]. See Arnell: 109 (1963).

S. harveyana Taylor: 408 (1846). Type: Cape of Good Hope, leg.: W.H. Harvey (FH, holo.; NY, S, W, iso.). [Syn. fide Sim: 33 (1926)].

Terricolous, on damp soil; thallus, mostly erect, dendroid shoots in loose mats or tufts, green to olive-green, medium-sized; proximal branches, after initial dichotomy, single, ± 4 mm long, then a further 2 or 3 times dichotomously furcate, with 7 or 8(–12) terminal branches, linear to narrowly ovate, up to 11 mm long, 1.6–2.0 mm wide, 125 μ m thick over ventrally slightly bulging costa, lacking rhizoids, but with central, brown conducting strand clearly visible and forking at dichotomies; apex rarely progressively narrowed with a reversion to stipe-like condition and arching down, mostly entire or slightly to deeply notched, bearing 2-celled slime papillae, margins of wings dentate, lacking slime papillae, plane, not undulating or hardly so, bilaterally expanded from ascending wingless stipe (Figure 1H), 4–18 mm long, in transverse section $275 \times 500 \mu$ m, arising from horizontally creeping and much branched, cylindrical brown rhizome, with numerous smooth ventral rhizoids, $\pm 12.5 \mu$ m wide. Wings generally unistratose, but medianly bistratose and grading into flattish costa (Figure 1K), laterally with marginal teeth, remote or closer together, occasionally very blunt, usually with 2(or 3) forwardly directed cells, diverging at an angle of $\pm 45^\circ$, basal cell $62.5 \times 37.5 \mu$ m (rarely with 2 adjacent cells), top cell bluntly conical, $50 \times 30 \mu$ m; marginal cells \pm rectangular to polygonal (40.0 – 67.5 – 90.0×27.5 – 37.5μ m, 30 – 35μ m thick in transverse section, their walls and those of 1(or 2) rows of inframarginal cells generally somewhat thicker (Figure 1J), coloured pinkish; laminal cells arching toward margins, polygonal, up to $82.5 \times 55.0 \mu$ m; epidermal cells along costa narrowly rectangular or long-hexagonal, 75.0 – $125.0 \times 37.5 \mu$ m, occasionally bearing 2-celled slime papillae above; chloroplasts numerous, $\pm 5 \mu$ m wide,

* National Botanical Institute, Private Bag X101, Pretoria 0001.
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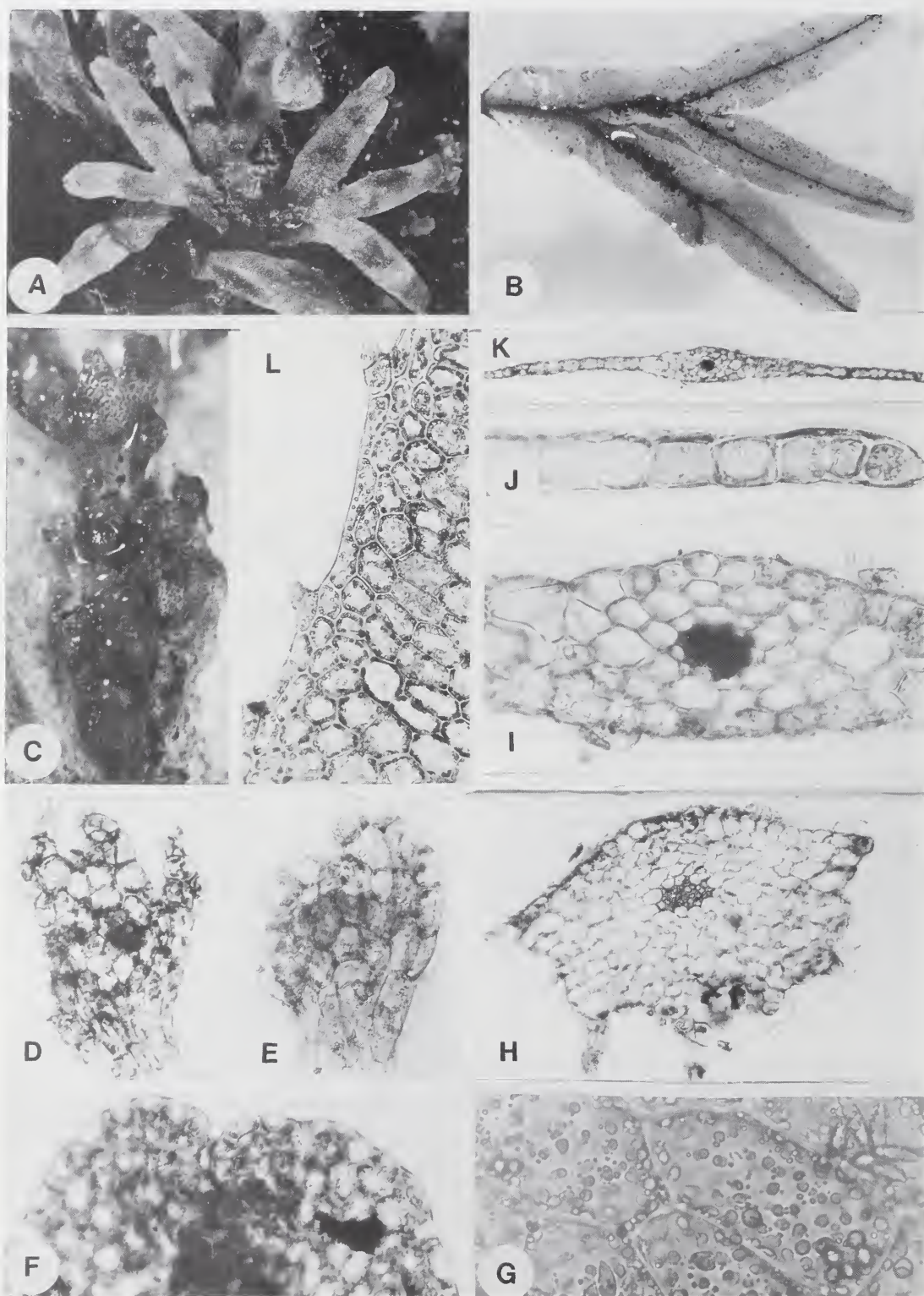


FIGURE 1.—*Symphyogyna podophylla*, plants and androecia. A, male branches in situ; B, branches with rows of antheridial scales along costa, C, some antheridial scales above costa, much enlarged; D, E, excised antheridial scales; F, apex of lobe; G, laminal cells with numerous round chloroplasts and few spindle-shaped oil bodies; H, transverse section of stipe; I, transverse section of costa and central conducting strand, much enlarged; J, transverse section of lateral and thicker-walled marginal cells of lobe; K, transverse section of lobe; L, toothed margin of lobe from above. A–F, H–L, *Koekemoer 991*; G, *Koekemoer 994*. A, $\times 4$; B, $\times 5$; C, $\times 70$; D, E $\times 100$; F, H, L, $\times 125$; G, $\times 500$; I, J, $\times 250$; K, $\times 50$. A–L, LM photographs.

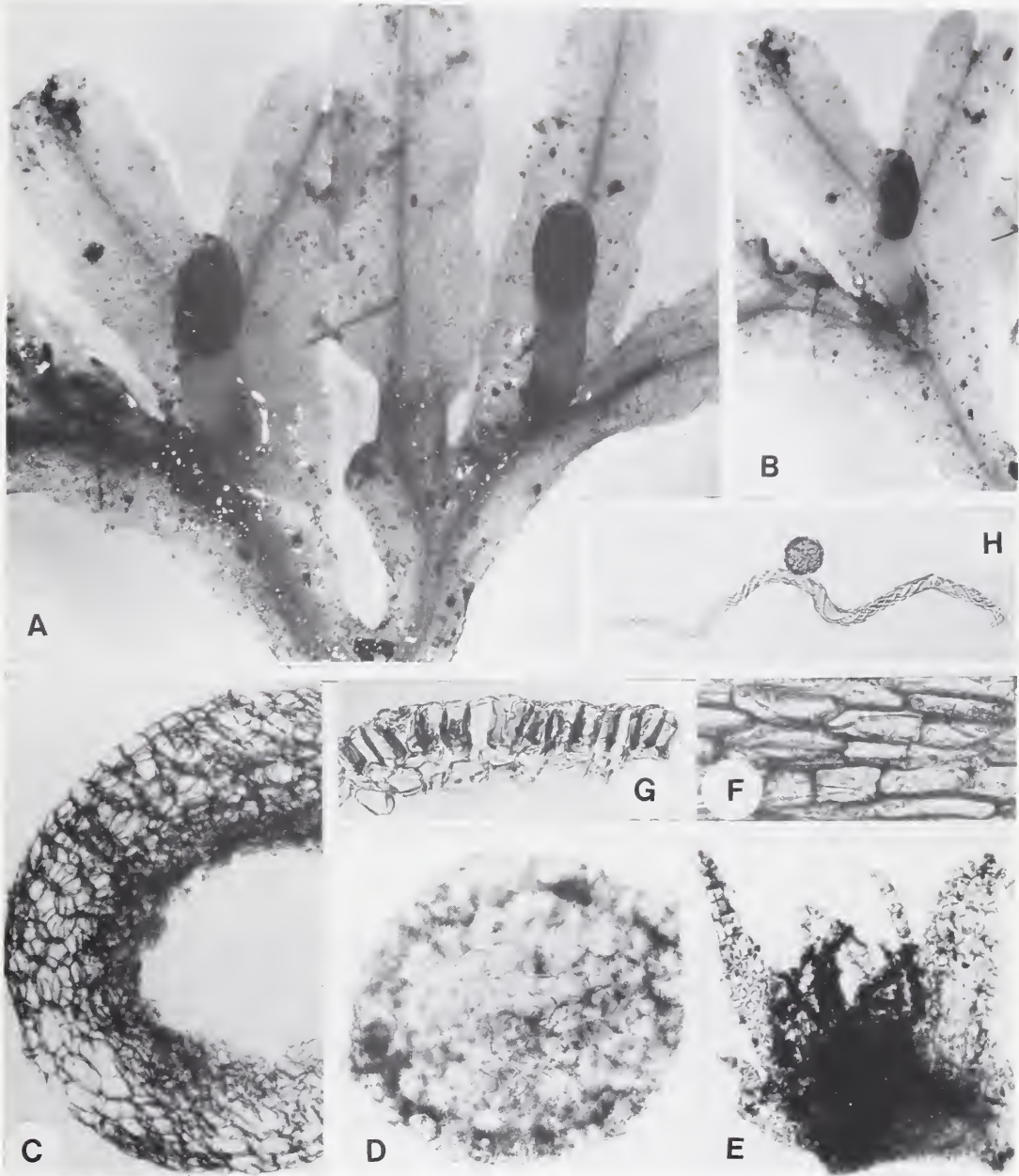


FIGURE 2. —*Symphyogyna podophylla*, female plants. A, B, female branches with capsules above bifurcation of costa; C, part of shoot calyptra in transverse section; D, young seta in transverse section; E, involucral scale and cluster of archegonia; F, outer cells of capsule wall; G, transverse section of capsule wall; H, spore and elater. A–G, *Koekemoer 991*. A, $\times 10$; B, $\times 8$; C, $\times 100$; D, $\times 125$; E, $\times 50$; F, G, $\times 250$. A–G, LM photographs.

entirely filling cells, or clustered along cell walls, several oil bodies also present, spindle-shaped (Figure 1G) and $\pm 7.5 \mu\text{m}$ long, or round when viewed end-on. *Costa* with central conducting strand, $37.5 \times 50.0 \mu\text{m}$, consisting mostly of 12 small, $\pm 10 \times 10 \mu\text{m}$, brown, thick-walled, angular cells, surrounded above and below by 3 rows of larger, thin-walled parenchymatous cells (Figure 1I), $20.0\text{--}22.5 \times 25.0\text{--}37.5 \mu\text{m}$.

Dioicous. *Androecia* in 1 or 2 dorsal rows over the costa (Figure 1A–C); antheridia $200 \times 175 \mu\text{m}$, short-stalked,

each one individually covered and well hidden by irregularly shaped, forwardly directed scale-like involucre (Figure 1D, E), $175 \mu\text{m}$ wide at base, up to $450 \mu\text{m}$ long, irregularly incised at apex. *Gynoecia* generally 2 per frond, dorsally situated above costa at bifurcation of conducting strand (Figure 2A, B), containing several archegonia and subtended by posteriorly inserted involucre (Figure 2E), $675 \mu\text{m}$ wide at base, deeply lacinate to filiform above, cells short- to long-rectangular, $45.0\text{--}125.0 \times 27.5\text{--}47.5 \mu\text{m}$. *Calyptra* thickening and enlarging into a fleshy shoot calyptra, $\pm 4 \text{ mm}$ long and up to 8 cell

rows or 250 μm thick in transverse section (Figure 2C), with several unfertilized archegonia remaining attached near the top (Figure 2A). *Capsule* cylindrical, $1800 \times 850 \mu\text{m}$, opening along several longitudinal valves, remaining attached above, wall brown, 2 cell layers thick (Figure 2G), outer cells elongate (Figure 2F), $62.5\text{--}107.5 \times 17.5 \mu\text{m}$, walls thickened, inner cells thin-walled. *Seta* erect when young, 480 μm in diameter, with ± 36 cortical cells, $\pm 50.0 \times 32.5 \mu\text{m}$, medullary cells slightly larger, $62.5 \times 37.5 \mu\text{m}$, angular, thin-walled (Figure 2D). *Spores* light brown, \pm globular, 20–25 μm in diameter, ornamentation nodular, with some very irregular, broad flattened granular ridges (Figure 3A–C), meshes sometimes distinct, but mostly not; proximal face with small round area with compact, punctate ornamentation (Figure 3D, E). *Elaters* brown, hardly tapering toward ends, $305\text{--}330 \times 7.5 \mu\text{m}$, 2-spiral (Figures 2H; 3F).

Symphyogyna podophylla is quite rarely collected in the Transvaal and Natal, but fairly frequently in southwestern, southern and eastern Cape. There are no records from the Orange Free State (Figure 4). From other parts of Africa, Arnell (1960) has reported it from Ethiopia (= Abyssinia) and Vanden Berghen (1965) has also been reported it from Ethiopia (= Abyssinia) as well as from Tanzania and the Congo Republic (Kivu Province). Best (1990) records both *S. podophylla* as well as its synonym, *S. harveyana*, from Zimbabwe. Váňa *et al.* (1979) report *S. podophylla* from Zaïre, Rwanda and Réunion; Bizot & Pócs (1974) found it to occur in Kenya on Mt Kenya and the Aberdare Mountains in montane mossy forests and subalpine moorland; Bizot *et al.* (1976) report it from Malawi. Some of these specimens may, however, belong to *Jensenia spinosa* (= *Pallavicinia spinosa*), with which *S. podophylla* has sometimes been confused (Grolle 1979).

DISCUSSION

In such a wide ranging species one would expect some local variation. A Sim specimen, *PRE-CH 1491*, from Table Mountain has bistratose wing margins, and medianly there are four layers of cells. The determination was kindly confirmed by Dr Grolle. Arnell (1963) regarded the size of the marginal teeth in *S. podophylla* as having no taxonomic significance, nor the thickness of the walls in the marginal cells. He also did not find distinct differences between the erect and procumbent forms, there being a continued gradation between the two.

In a comparison of transverse sections taken at the middle of the apical lobes of specimens of *S. podophylla* and of *S. hymenophyllum* from Juan Fernandez, Arnell (1956) stated that the thickness of the 'nerves' and the size of the teeth in the margin of the thalli vary but little. Arnell (1963) also compared specimens of *S. hymenophyllum* from Tristan da Cunha and Inaccessible Island as well as from Réunion and from Kilimanjaro, with numerous specimens of *S. podophylla* from the Cape (e.g. Thunberg's collections) and could not find any real difference between them. On the other hand, Gottsche *et al.* (1846) distinguished *S. podophylla* from *S. hymenophyllum* by the 'frondis laciniis basi attenuatis subpetiolatis' of the former.

In the present study, a photograph of the transverse section of a lobe (Figure 1K) was compared with the drawing of a section, taken midway of a terminal lobe, by Hässel de Menéndez (1961a: fig. 10c) and the resemblance is unmistakable. It may thus be that Arnell (1963) was indeed correct in placing *S. hymenophyllum* in synonymy under *S. podophylla*. Scott (1985) also recognizes the Australian species as *S. podophylla*. Should

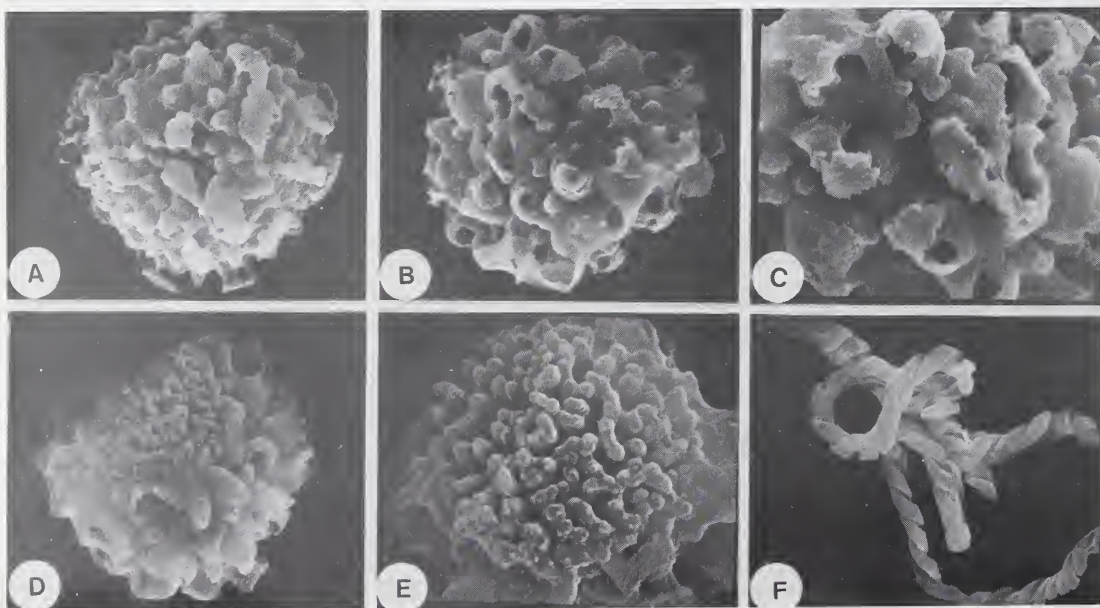


FIGURE 3.—*Symphyogyna podophylla*, spores and elaters. A, B, distal face; C, distal face much enlarged; D, part of proximal face with punctate area; E, punctate area on proximal face, much enlarged; F, elaters. A, *Koekemoer 991*; B–E, *Doidge 168*; F, *Hilner CH 1499*. A, $\times 1835$; B, D, $\times 1530$; C, E, $\times 2524$; F, $\times 720$.

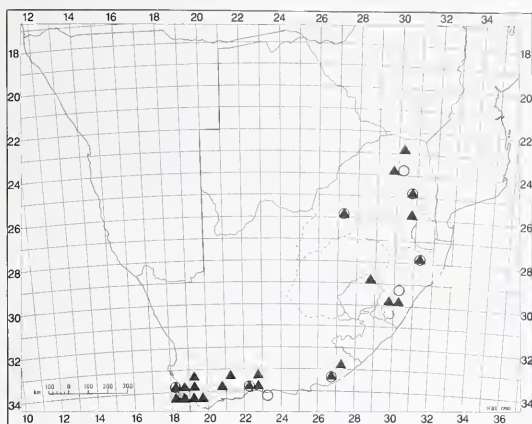


FIGURE 4.—Distribution of *Symphyogyna podophylla*, ▲, and *Pallavicinia lyellii*, ○, in southern Africa.

S. podophylla and *S. hymenophyllum* eventually conclusively prove to be conspecific, then *S. podophylla* would be circumsubantarctic in its range, since *S. hymenophyllum* is reported to occur in South America, and New Zealand is the type locality. Pócs (1976), in discussing the presence of subantarctic bryophytes in tropical Africa, remarks on the high number of subantarctic elements that are present and reckons that they may have migrated northwards by means of mountain hopping.

Symphyogyna podophylla is a less common and smaller plant than *S. brasiliensis*. It can be distinguished by: its growth form which is generally flabellate from an erect stalk arising from a creeping rhizome; the lobe margins which are toothed and hardly undulate; it rarely fruits and the spore ornamentation is characterised by broad, flat, roughened, irregular ridges, sometimes forming 'loops', and not by narrow, erect ridges as in *S. brasiliensis*. *Symphyogyna podophylla* and *S. brasiliensis* are the only two species of *Symphyogyna* occurring in southern Africa and are placed in the subfamily Symphyogynoideae (Trev.) Grolle.

Note: the collector of the type specimens of *S. rigida* is stated to be Mildbraed by Stephani (1917) and Geissler & Bischler (1990). However, Mildbraed was the publisher of 'Wissenschaftliche Ergebnisse der Deutschen Zentral-Afrika-Expedition 1907–1908'; the leader of the expedition, Adolf Friedrich, Duke of Mecklenburg, should be cited as collector, as was done by Vanden Berghen (1965) and now by me.

SPECIMENS EXAMINED

TRANSVAAL.—2230 (Messina): Zoutpansberg, Piesanghoek, at Waterfall, (—CC), *M. Bosman* 206 (PRE); Piesanghoek, (—CC), *M. Bosman* 943 (PRE); Entabene, (—CC), *M. Bosman* 1774 (PRE); Entabene, (—CC), *Bottomley* 2865 (PRE); De Hoek State Forest, Grootbosch Hiking Trail, ± 9.5 km from start, (—CC), *Koekemoer* 991 (PRE); Zoutpansberg, (—CC), *Obermeyer* 1941C ex herb. Tvl. Museum, *Obermeyer* 3109 (PRE). 2329 (Pietersburg): Haenertsburg, (—DD), *H.A. Wager* CH 3808 (PRE). 2430 (Pilgrims Rest): Graskop, Fairland, (—DD), *Glen* 2982 (PRE); Hebron Mountain, in second cleft on plateau, against vertical stream wall, (—DB), *Vorster* 1000 (PRE); Hebron Mountain, northern slope, gallery forest along stream in plantation, on stone and soil, (—DB), *Vorster* 1635 (PRE); Mariëpskop, Blyde River footpath, on wet earth bank along stream in forest, (—DB), *Vorster* 1516

(PRE). 2527 (Rustenburg): Magaliesberg, lower Tonquani Kloof, cliff face, in dripping water, (—CA), *H. Anderson* 1249, 1250 (PRE); Magaliesberg range, Crystal Waters, 13 km E of Rustenburg, in constant drip of waters of sheer chasm, into a stream a few feet below, (—CA), *Mogg* 348/8 (PRE). 2530 (Lydenburg), Kaapsche Hoop, (—DB), *V.A. Wager* 62 (PRE).

NATAL.—2731 (Louwsburg): Zululand, Vryheid Dist., Ngoni Forest, (—CD), *Forester* CH 1505, CH 1529, CH 1530 (PRE). 2828 (Bethlehem): Mont-aux-Sources, (—DD), *Doidge* 168 (PRE). 2929 (Underberg): Donnybrook, Gala Bush, (—DD), *Doidge* CH L3112 (PRE). 2930 (Pietermaritzburg): Edendale, Gordon Falls, (—CB), *T.R. Sim* CH 1495 (PRE); Hilton Road, (—CB), *T.R. Sim* 8242 (PRE).

CAPE.—3227 (Stutterheim): Hogsback, Victoria East, (—CA), *Van der Bijl* 75 (PRE); Hogsback, in shade, streambank, (—CA), *Young* CH 1507 (PRE); Evelyn Valley, (—CB), *T.R. Sim* CH 1522 (PRE). 3318 (Cape Town): Table Mountain, Disa Gorge, (—CD), *S. Arnell* 1059, 1099, 3932 (PRE); Table Mountain, Window Gorge, (—CD), *Bews* CH 1517 (PRE); Table Mountain, Skeleton Gorge, (—CD), *Bews* 8482 (PRE); top of Table Mountain, (—CD), *Bews* 8516 (PRE); Table Mountain, Woodhead Tunnel Gorge, (—CD), *Bews* 8519 (PRE); in spring at base of Lion's Head, (—CD), *Bews* CH 1490 (PRE); Table Mountain, (—CD), *Bulus* CH 1496 (PRE); Table Mountain, Skeleton Ravine, (—CD), *Bulus* CH 1521 (PRE); Table Mountain, (—CD), *Michell* CH 1489 (PRE); eastern slopes of saddle between Table Mountain and Devil's Peak, on wet and partly shaded rocks, (—CD), *Pillans* 3548 (PRE); Devil's Peak, The Grottoes, (—CD), *T.R. Sim* CH 1492 (PRE); Table Mountain, Window Gorge waterfall, (—CD), *T.R. Sim* CH 1493 (PRE); Table Mountain, Slongoli, (—CD), *T.R. Sim* CH 1494 (PRE); Table Mountain, Woodhead tunnel intake, (—CD), *T.R. Sim* CH 1506 (PRE); Cape Town, Platteklip stream, (—CD), *T.R. Sim* CH 1511 (PRE); Newlands ravine, (—CD), *T.R. Sim* CH 1527, CH 1528 (PRE); Table Mountain, (—CD), *H.A. Wager* 4 (PRE). Without locality, *H.A. Wager* 3828 (PRE); Stellenbosch, Paradise Ravine, growing in dense masses, (—DD), (label in Duthie's handwriting), ex Herb., *Sim* CH 1510 (PRE); Stellenbosch Mountain, above Brandwacht, lower slopes facing west, wet streamside, (—DD), *Oliver* 9028 (PRE). 3319 (Worcester): Tulbagh Dist., Sneeuwgat Valley, (—AA), *Thorne* CH 2877 (PRE); Groot Drakenstein Mountains, (—CC), *Primos* CH 1504 (PRE). 3320 (Montagu): Tradouw Pass, S of Barrydale near waterfall in forested kloof, (—DC), *Magill* 6174 (PRE). 3321 (Ladismith): Seven Weeks Poort, (—AD), *Thorne* CH 1543 (PRE). 3322 (Oudtshoorn): Meiring-spoort, in deep shade in cracks of vertical rock wall, almost under waterfall, (—BC), *Jacobson* 2253 (PRE); Montagu Pass, wet rock face near Stinkhoutdraai, (—CD), *S.M. Perold* 1547 (PRE); The Wilderness, George, (—CD), *Taylor* CH 1519 (PRE); Saasveld, Groeneweide, (—DC), *Koekemoer* 994 (PRE). 3326 (Fort Beaufort): near Grahamstown, Paradise Kloof, Coldstream, (—BC), *Hilner* CH 1499 (PRE). 3327 (Stutterheim): Hogsback, (—CA), *Van der Bijl* CH 1497 (PRE); Hogsback, in shade, streambank, (—CA), *Young* CH 1507 (PRE); Evelyn Valley, (—CB), *T.R. Sim* CH 1522 (PRE). 3418 (Simonstown): kloof near Chaplin Point, (—AB), *T.R. Sim* CH 1501 (PRE); Kogelberg, near Gordon's Bay, (—BB), *Mogg* CH 939 (PRE); Hottentot Hollands Mts, (—BB), *Thorne* CH 3096 (PRE). 3419 (Caledon): Riviera Kloof, Hermanus Dist., (—AC), *Louwrens* CH 2889 (PRE); Mossel River, (—AD), *Potts* 26 (PRE); Oudebos, Zonder Einde, (—BB), *Thorne* CH 3106 (PRE).

Pallavicinia lyellii (Hook.) Carruth. in Journal of Botany, British and Foreign 3: 302 (1865) (*Pallavicinius*); Sim: 32 (1926); Müller: 519 (1951–1958); Hässel: 264 (1961b); Hodgson: 223 (1968); Grolle & Piippo: 60 (1986).

Jungermannia lyellii Hook.: tab. 77 (1816). Type: England, Hampshire, New Forest, 'Cadman bog', 6 May 1812, *Lyell* (BM, lecto, fide Grolle & Piippo 1986).

Pallavicinia pilifera Steph.: 271 (1891); Steph.: 10 (1900); Arnell: 112 (1963); Vanden Berghen: 164 (1965). Type: W Africa, Sao Tomé Island, *Quintas* (G 12058) (G, holo.; G, M, S, W, syn.). Synonymy fide Vanden Berghen: 150 (1972).

For detailed synonymy see Grolle & Piippo (1986).

Terricolous, growing on damp soil; thallus, prostrate and creeping (Figure 6A), in crowded, overlying, caespitose mats, dark green, mostly simple, occasionally dichotomously branched, or ventrally from the midrib, medium-sized to large, up to 60 × (2.0–)4.0–6.5 mm, 320–350 µm thick over ventrally bulging costa from

which, at intervals, arise dense reddish brown, smooth, translucent rhizoids $12.5\text{--}20.0\text{ }\mu\text{m}$ wide; central conducting strand brown, clearly visible from above, forking at dichotomies; apex entire or with shallow notch, bearing 2-celled slime papillae (Figure 5F), also along margins of wings, which are undulating, almost entire or with remote teeth, expanded bilaterally from wingless stipe, $375 \times 750\text{ }\mu\text{m}$ in transverse section. *Wings* unistratose,

bordered by a row of mostly long-rectangular or 5-sided cells ($27.5\text{--}50.0\text{--}62.5 \times 27.5\text{--}45.0\text{ }\mu\text{m}$, marginal teeth generally small and blunt (Figure 5D), only 1- or 2-celled, $25.0 \times 37.5\text{ }\mu\text{m}$, toward apex often larger, up to 5-celled, forwardly directed (Figure 5E); laminal cells polygonal, some hexagonal, $57.5\text{--}87.5 \times 27.5\text{--}45.0\text{ }\mu\text{m}$, in transverse section $42.5\text{ }\mu\text{m}$ thick, containing numerous chloroplasts, $5.0\text{--}7.5\text{ }\mu\text{m}$, oil bodies green, nodular, 8–12 per cell

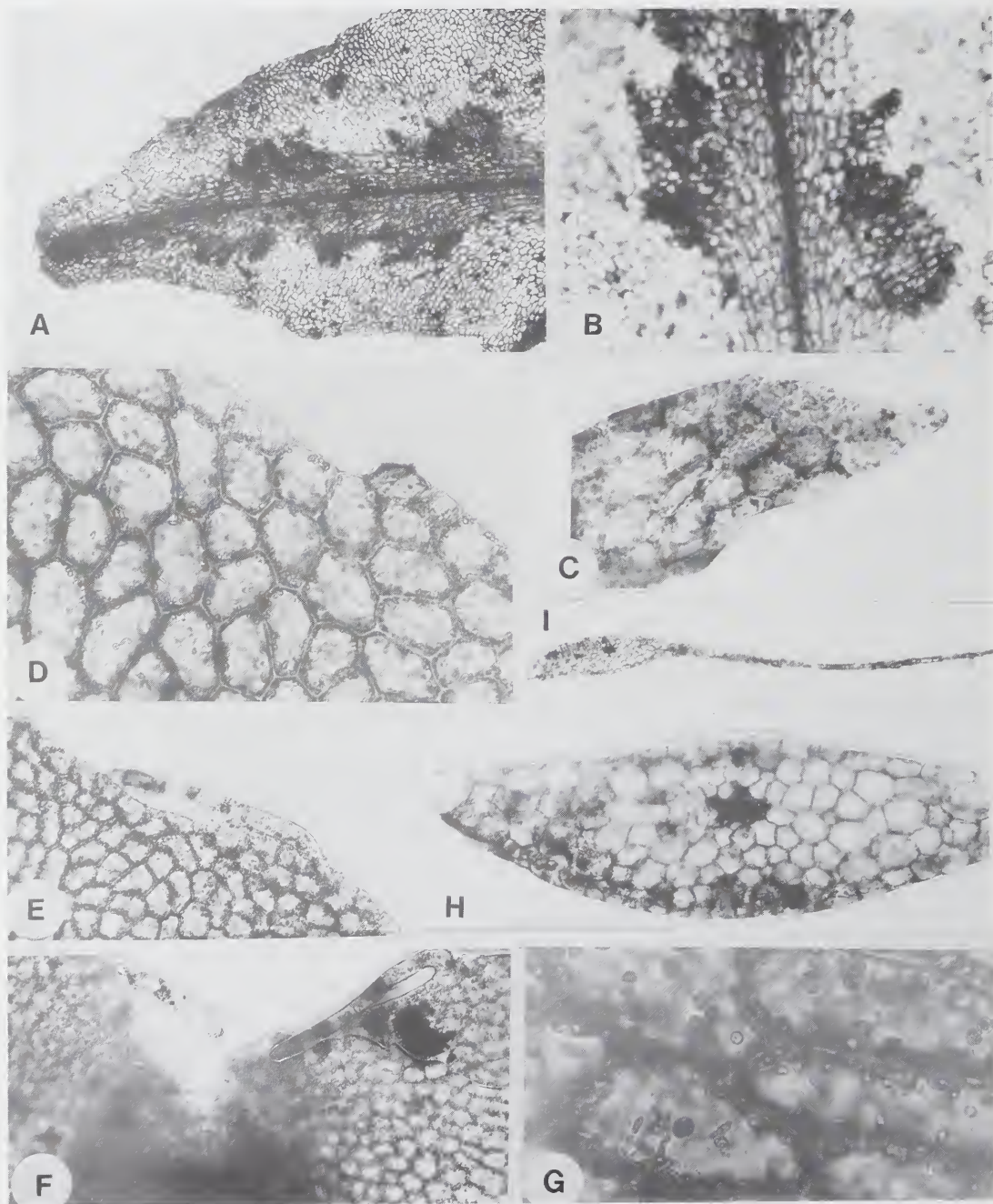


FIGURE 5. — *Pallavicinia lyellii*, plants and androecia. A, male branch with androecia laterally situated above costa; B, male scales more enlarged; C, part of male scale, excised; D, margin of lobe, with blunt tooth; E, long marginal tooth, near apex; F, notched apex with 2-celled slime papillae, and long marginal teeth; G, laminal cells from above, containing chloroplasts and rod-like oil bodies; H, transverse section of costa and central conducting strand, much enlarged; I, transverse section of costa and wing on one side only. A–C, *Glen* 2882; D–I, *Koekemoer* 990. A, $\times 30$; B, $\times 70$; C, $\times 165$; D, $\times 250$; E, F, H, $\times 125$; G, $\times 500$; I, $\times 25$.

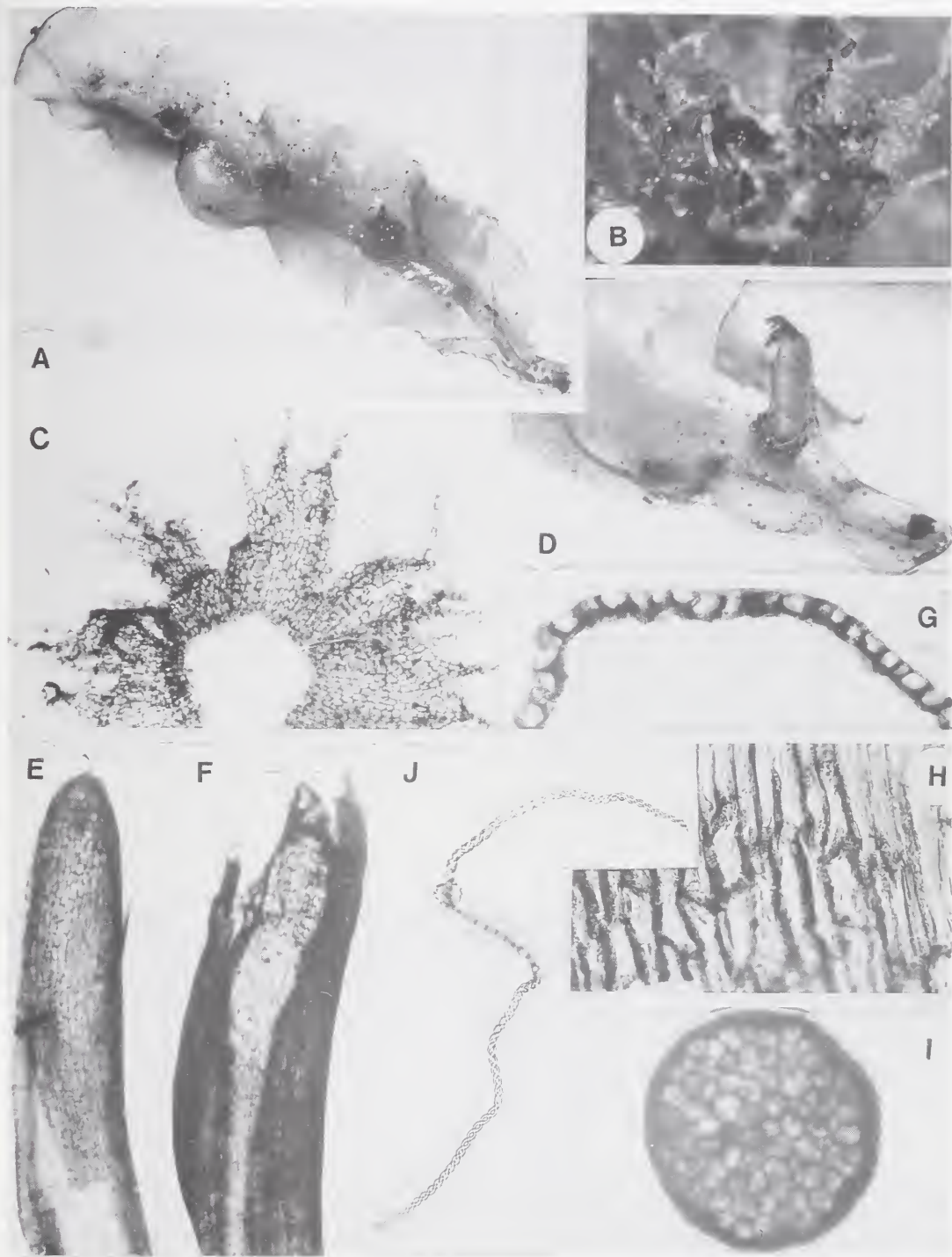


FIGURE 6. — *Pallavicinia lyellii*, female plants. A, lobe with gynoeceia along costa; B, involucre much enlarged; C, opened involucre spread out; D, lobe with capsule still enclosed in pseudoperianth; E, calyptra; F, pseudoperianth; G, transverse section of capsule wall; H, outer cells of capsule wall; I, transverse section of seta; J, elater and spore. A–C, *Koekemoer 990*; D–F, I, *Glen 2882*; G, H, J, *Arnell 2084*. A, $\times 5.5$; B, $\times 55$; C, $\times 70$; D, $\times 11$; E, F, $\times 30$; G, H, J, $\times 250$; I, $\times 80$.

(Figure 5G), up to 7.5 μm long, thin, others seen end-on and round. *Costa* abruptly grading into wings, overlying epidermal cells long-rectangular, 65–110 \times 21–30 μm , sometimes with slime papillae, central conducting strand

50 \times 80–125 μm , consisting of about 32 small, \pm 10 μm wide, thick-walled, angular brown cells, surrounded by larger, 35–55 μm wide, thin-walled parenchymatous cells, 3 rows above and 4 or 5 rows below (Figure 5H).

Diocious. *Androecia* in 2 parallel dorsal rows, one on either side of costa (Figure 5A), each a flat band raised shelflike $\pm 100 \mu\text{m}$ above lamina and $\pm 280 \mu\text{m}$ wide, laterally at free margin, expanded into confluent scales, directed transversely to long axis of shoot (Figure 5B), $210 \times 200 \mu\text{m}$, with laciniae (1-)2- or 3-celled (Figure 5C), $\pm 150 \times 40 \mu\text{m}$; antheridia globular, $170 \mu\text{m}$ wide, short-stalked and individually placed, hidden by covering scale, central area above midrib lacking antheridia and scales. *Gynoeceia* up to 4 or 5 per frond (Figure 6A), acropetally arranged and dorsally situated at intervals along costa, involucre 3–5 layers thick, cup-like, base $\pm 900 \mu\text{m}$ high, mouth densely fringed with ciliate laciniae up to $750 \mu\text{m}$ long (Figure 6B, C), enclosing a group of 20–30 archegonia. *Pseudoperianth* 6 mm long, tubular (Figure 6F), apex brownish, long-piliferous (Figure 6D), developing after fertilization of an archegonium; calyptra (Figure 6E) bistratose, initially enveloping capsule and seta, several unfertilized archegonia flattened against sides and at base, old archegonial neck retained at tip. *Capsule* oblong-cylindrical, 2.3–3.7 mm long, opening along several valves; wall yellow-brown, 2 cell layers thick (only 1 shown in Figure 6G); outer cells elongate, $87.5\text{--}150.0 \times 12.5\text{--}22.5 \mu\text{m}$, lacking semi-annular thickenings (Figure 6H). *Seta* with slight swelling at foot, eventually up to 9 mm long, sinuate, $500 \mu\text{m}$ in diameter, cortical cells darker, one cell deep, $\pm 35 \times 35 \mu\text{m}$, in 45 cell rows; medullary cells ± 70 , $\pm 35\text{--}60 \mu\text{m}$ wide (Figure 6I). *Spores* light brown, \pm globular, $17.5\text{--}23.0 \mu\text{m}$ in diameter, ornamentation reticulate with larger areolae on distal face $\pm 5 \mu\text{m}$ wide, further subdivided into smaller areolae by finer walls (Figure 7A–D); proximal face with only smaller, irregular areolae (Figure 7C–E). *Elaters* light brown, tapering toward ends, up to $470 \mu\text{m}$ long, $7.5 \mu\text{m}$ thick, bispiral (Figures 6J; 7F).

DISCUSSION

Pallavicinia lyellii is widely distributed and regarded as subcosmopolitan. In southern Africa it is known from

northern and central Transvaal, Natal, and southwestern, southern and eastern Cape (Figure 4), but not many collections have been made. It is probably more common, but is undercollected.

The very large number of synonyms listed by Grolle & Piippo (1986) are an indication of its variability, resulting from its plasticity. Fertile plants are rare, with male plants generally smaller and abruptly narrowing to the apex of the lobe. The marginal teeth are quite variable: mostly small and blunt, but sometimes up to 5 cells long. In colour, plants are a deeper green than those of *Symphyogyna* species and further differ by the androecial arrangement, by the cup-like involucre, short calyptra, the presence of a pseudoperianth and by the spore ornamentation. The plants described and illustrated as *Pallavicinia lyellii* by Sim (1926) are clearly those of *Symphyogyna brasiliensis*.

SPECIMENS EXAMINED

TRANSVAAL.—2330 (Tzaneen): De Hoek State Forest, Grootbosch Hiking Trail, $\pm 6.5 \text{ km}$ from starting point, (–CC), *Koekemoer* 990 (PRE). 2430 (Pilgrim's Rest): Graskop, Fairyland, occasionally on dry stream bank, (–DD), *Glen* 2975 (PRE); Mariepskop, Blyde River footpath, on sandstone slab in forest, (–DB), *Vorster* 1499 (PRE). 2527 (Rustenburg): Rustenburg Nature Reserve, Cederbergkloof near Utopia, (–CA), *Koekemoer* 971 (PRE).

NATAL.—2731 (Louwsburg): Louwsburg Dist., Ngome Forest, Cetshwayo waterfall walk, (–CD), *Glen* 2882 (PRE). 2930 (Pietermaritzburg): Blinkwater, (–AB), *J.M. Sim* CH 1456 (PRE).

CAPE.—3318 (Cape Town): Table Mountain, (–CD), *Michell* CH 1481 (PRE). 3322 (Oudtshoorn): George, Van Riebeeck Gardens, on damp streambank, (–CD), *S.M. Perold* 927 (PRE). 3326 (Grahamstown): Paradise Kloof, Cold spring, near Grahamstown, (–BC), *Hilner* CH 1478 (PRE). 3423 (Knysna): Knysna, Buffels Nek, streamside, (–AA), *S. Arnell* 1515 (PRE); Knysna, Garden of Eden, (–AA), *S. Arnell* 2084 (PRE).

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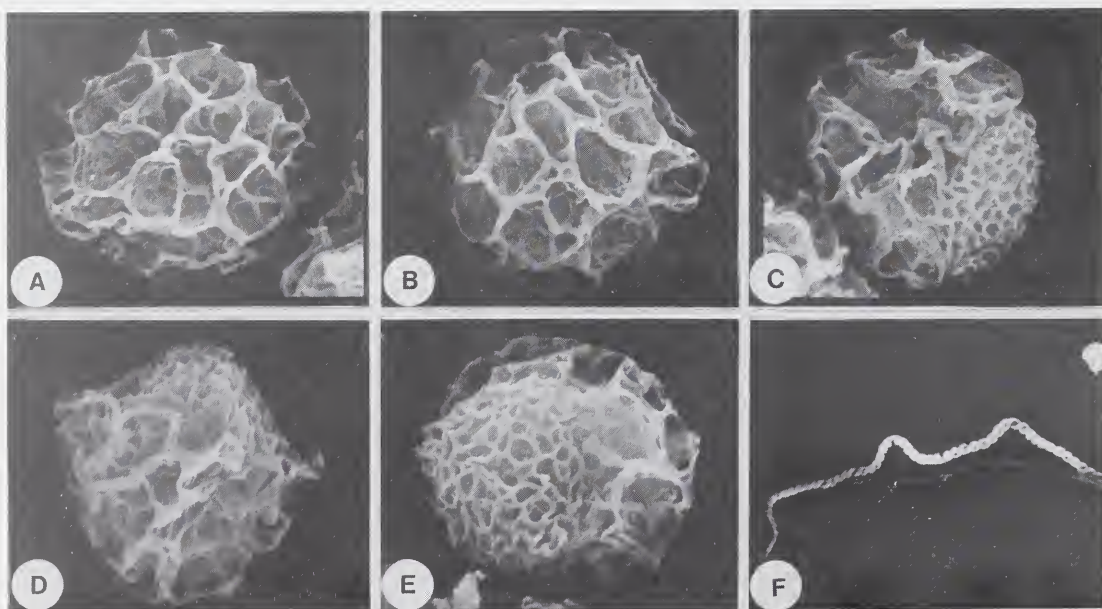


FIGURE 7.—*Pallavicinia lyellii*, spores and elaters. A, B, distal face; C, D, side view; E, proximal face; F, elater. A–F, *S. Arnell* 2084. A, B, D, $\times 1850$; C, E, $\times 1905$; F, $\times 189$.

and for their helpful suggestions; to my colleagues at NBI, Ms Koekemoer and Dr H.F. Glen, for collecting specimens; to Mrs A. Romanowski, photographer, for developing and printing the photographs (taken by the author) and to Mrs J. Mulvenna, typist, for her valued contribution.

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A biosystematic study of *Pentameris* (Arundineae, Poaceae)

N.P. BARKER*

Keywords: Arundineae, Arundinoideae, cladistics, conservation status, cytology, leaf anatomy, *Pentameris*, phylogeny, systematics

This paper is dedicated to the memory of Lucy K.A. Crook (née Chippindall)

ABSTRACT

A biosystematic study of the endemic southwestern Cape grass genus *Pentameris* Beauv. is presented. Results of studies on the macro- and micromorphology, leaf blade anatomy and cytology are discussed and illustrated. The results of a cladistic study indicate that the genus is monophyletic, united by the synapomorphies of ovary and fruit characters. The conservation status of the taxa in the genus is assessed, and conservation status codes allocated. A key to the taxa in the genus is presented, and each species is described. Five new species, *Pentameris glacialis* N.P. Barker, *P. hirtiglumis* N.P. Barker, *P. oreophila* N.P. Barker, *P. swartbergensis* N.P. Barker and *P. uniflora* N.P. Barker, and one new subspecies, *P. longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker, are described and illustrated.

UITTREKSEL

'n Biosistematiese ondersoek van die endemiese Suidwes-Kaapse grasgenus *Pentameris* Beauv. word aangebied. Resultate van ondersoeke op die makro- en mikromorfologie, blaarskyfanatomie en sitologie word bespreek en geïllustreer. Die resultate van 'n kladistiese ondersoek dui daarop dat die genus monofileties is, verenig deur die afgeleide kenmerke van die vrugbeginsel en vrug. Die bewaringstatus van die taksons in die genus word geraam en bewaringstatuskode toegeken. 'n Sleutel tot die taksons in die genus word aangebied, en elke spesie word beskryf. Vyf nuwe spesies, *Pentameris glacialis* N.P. Barker, *P. hirtiglumis* N.P. Barker, *P. oreophila* N.P. Barker, *P. swartbergensis* N.P. Barker en *P. uniflora* N.P. Barker, en een nuwe subspesie, *P. longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker, word beskryf en geïllustreer.

CONTENTS

Introduction	25
Morphology	25
Leaf blade anatomy	29
Microhairs	29
Abaxial macrohairs	29
Adaxial macrohairs	30
Prickles	30
Cytology	31
Phylogeny	31
Choice of outgroup	31
Character distribution	32
Taxonomic implications	33
Conservation status	33
Taxonomy	33
Acknowledgements	44
References	46

INTRODUCTION

The genus *Pentameris* Beauv. occurs in the winter rainfall region of the Cape Province, South Africa, where it is restricted to soils derived from Table Mountain Sandstone or the shale bands associated with this geology. It may therefore be considered an endemic of the Cape Flora (Goldblatt 1978). All known species of the genus are perennial C₃ plants.

The genus was erected by Palisot de Beauvois in 1812 on the basis of a specimen sent to him by Du Petit-Thouars. No collection number or locality is provided in this description. However, it is known that Du Petit-Thouars,

a French traveller and botanist, obtained material from the Cape during a visit in February 1793 (Gunn & Codd 1981). The genus name is Greek, meaning 'five parts', probably a reference to the apical region of the lemma which is divided into what Palisot De Beauvois (1812) described as four bristles (two of which may be more accurately described as lemma lobes) and a central awn.

Only one species is mentioned under the generic description: *P. thuarii* Beauv. (Palisot de Beauvois l.c.). This single species was subsequently placed in *Danthonia* DC. by a number of early taxonomists (Desvaux 1831; Nees 1841; Steudel 1855; Durand & Schinz 1895), whereas others retained it in the genus *Pentameris* (Roemer & Schultes 1817; Kunth 1833, 1835). Stapf (1897) expanded the genus *Pentameris* to include four other taxa, all characterised by fruit with a free pericarp. Chippindall (1955) retained the genus in this format, but incorporated two nomenclatural corrections published by Schweickardt (1938). Gibbs Russell *et al.* (1985) list these five taxa as *Pentameris dregeana* Stapf, *P. longiglumis* (Nees) Stapf, *P. macrocalycina* (Steud.) Schweick., *P. obtusifolia* (Hochst.) Schweick. and *P. thuarii* Beauv.

However, the unusual leaf blade anatomy (Ellis 1985d; Barker 1990) and fruit morphology (Barker 1986, 1989, 1990) of *P. obtusifolia* places this species within the genus *Pseudopentameris* Conert (Barker in prep.a). *Pentameris obtusifolia* is therefore not further considered in this study.

MORPHOLOGY

The basal parts of all the species are woody, but the woolly and/or swollen underground parts that occur in certain species of *Pentaschistis* (Nees) Spach and *Merxmüllera* Conert are absent. The species are generally tufted, with stems sometimes branching, but generally only

* National Botanical Institute, Private Bag X101, Pretoria 0001. Present address: Botany Department, University of Cape Town, Private Bag, Rondebosch, Cape Town 7700.
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in the basal quarter. In older plants branching results in a cushion or a bush-like growth form. These branched structures are referred to here as 'culms', although they do not possess typical culm anatomy. Instead, the anatomy resembles that of a rhizome (H.P. Linder pers. comm.). The term 'aerial culm' will be used here to denote the annually produced, few-noded structure which terminates in an inflorescence.

In *P. thuarii*, branching can occur at any node on the culm, and some specimens comprise long, decumbent, scandent or vertical culms with many shorter vegetative and reproductive branches arising from the upper regions. Such branching from cauline innovation shoots results in an 'evergreen', perennial plant, which takes the form of a divaricate herb. This branching pattern might allow the plant to grow taller than species possessing only basal innovation shoots (Linder & Ellis 1990a). Branching and growth from cauline innovation shoots is also found in a few species of *Pentaschistis*, *Chaetobromus* Nees and *Pseudopentameris*. In the latter genus the branched condition may approximate the extreme development found in *Pentameris thuarii*.

The leaf structure of *Pentameris* is typical of the Arundineae. The leaf sheaths are persistent, although the leaf blades may not be. The older culms are thus frequently covered in the remains of sheaths from previous years of growth. These sheaths may be appressed to or free from the culm. The sheath indumentum varies between the species, ranging from glabrous to pubescent along the margins to uniformly pubescent (and sometimes woolly). These sheath characters are also found in other arundinoid genera. The ligule is, as in many other arundinoid genera, a fringe of hairs. The sheath mouth may be bearded in some species, but this, too, is not unusual. Two species, *P. thuarii* and *P. longiglumis* have fairly well-developed auricles. In the former species these are a characteristic purple or brown colour. The leaf blade varies in its internal and epidermal anatomy. Many characters are shared, although not consistently so, with taxa of *Pentaschistis*, and (to a lesser extent) *Merxmuellera*. Ellis (1985c, 1986; Ellis & Linder 1992), on the basis of leaf anatomical studies, is of the opinion that *Pentameris* is closely allied to *Pentaschistis*.

The inflorescence is a panicle which varies from compactly lanceolate to laxly globose. It must, however, be noted that the panicles of all the species are open and somewhat lax during the period of pollination. Before and after this period, the panicles contract to a lanceolate shape. Panicle shape is therefore difficult to describe as it depends on the reproductive phase of the plant at the time of observation or collection. This variation is also found in numerous other arundinoid taxa, for example *Pentaschistis* (Linder & Ellis 1990b). No spicate panicles are known from this genus.

The spikelets are two-flowered (one exception; *P. uniflora*), and the partially developed remains of a third floret may sometimes be present, particularly in *P. macrocalycina*. The two-flowered state is shared with the vast majority of the species in *Pentaschistis* (Linder & Ellis 1990b). When two florets are present, the basal floret is sessile, the apical floret pedicellate. The florets are otherwise morphologically identical, and both are hermaphroditic and fertile, as in *Pentaschistis*.

The lemma is generally nine- to eleven-nerved. The majority of the veins anastomose in the basal region of the central awn and the two lateral bristles. The lemma lobes on the outside of the bristles are variously adnate to the bristle, ranging from free (in *P. thuarii*) to almost completely adnate (in *P. macrocalycina*). The shape of this lobe is also variable, being acuminate, acute or dentate. Similar variation is found in *Pentaschistis* (Linder & Ellis 1990b). The central awn is geniculate in all species, the basal portion is flattened but twisted and shorter than the attenuating apical portion. The margin of both the basal and apical regions of the awn are finely serrated. This awn structure is shared with genera such as *Pentaschistis*, *Pseudopentameris*, *Merxmuellera* and *Chaetobromus* as well as the non-African genus *Danthonia*.

The palea is bicarinate, apically bilobed and pubescent between the veins. It exceeds the lemma body in length, but seldom exceeds the lemma lobes, a situation also found in species of *Pentaschistis*, *Pseudopentameris* and *Merxmuellera*.

The lodicules in certain arundinoid genera have been examined and used for taxonomic purposes (Tomlinson 1985). The lodicules of *Pentameris* are generally glabrous and cuneate, but differences have been noted in some specimens of *P. swartbergensis* and *P. distichophylla*. The lodicules in these species are generally apically ciliolate, and sometimes an arm-like extension arising from one of the lateral margins is present. Ciliolate lodicules are also known from species of *Pseudopentameris*, *Merxmuellera* and *Pentaschistis* (Linder & Ellis 1990b).

All species of the genus have three anthers, which are usually purple in colour. These vary in size in relation to the size differences of the florets, but this has not been incorporated as a taxonomically meaningful character.

The above morphological features can therefore not be used to clearly differentiate *Pentameris* from several other southern African arundinoid genera, notably *Pentaschistis*. There are, however, two micromorphological features which have, in the past, been used to distinguish *Pentameris* from all other southern African arundinoids. Both features are characters of fruit and ovary. Firstly, the fruit is an achene, and secondly, the fruit of all taxa possesses a dense tuft of hairs at the apex of the ovary. These hairs are retained in developing and mature fruit where they become reluctantly deciduous.

Stapf (1897: 512) separated *Pentameris* from *Pentaschistis* on the basis of fruit morphology: the crustaceous pericarp and free seed. He described the structure of the ovary as being '... so alike in the five species of this genus that it is very probable that they agree in the peculiarities of the ripe fruit which is known only in *P. thuarii*' and further stated that '... there is in *Pentaschistis* no approach to the characteristic structure of the ovary and the fruit of *Pentameris*'.

This unusual fruit type, the achene, is described by Clayton & Renvoize (1986) as a fruit with a thin, hard, free pericarp attached to the ovule in the region of the hilum. It is unusual in the tribe Arundineae, and is found in only three of the approximately 40 arundinoid genera worldwide. The fruits of the remaining arundinoid genera are described as caryopses or as caryopses with a variably separable pericarp (Clayton & Renvoize l.c.).

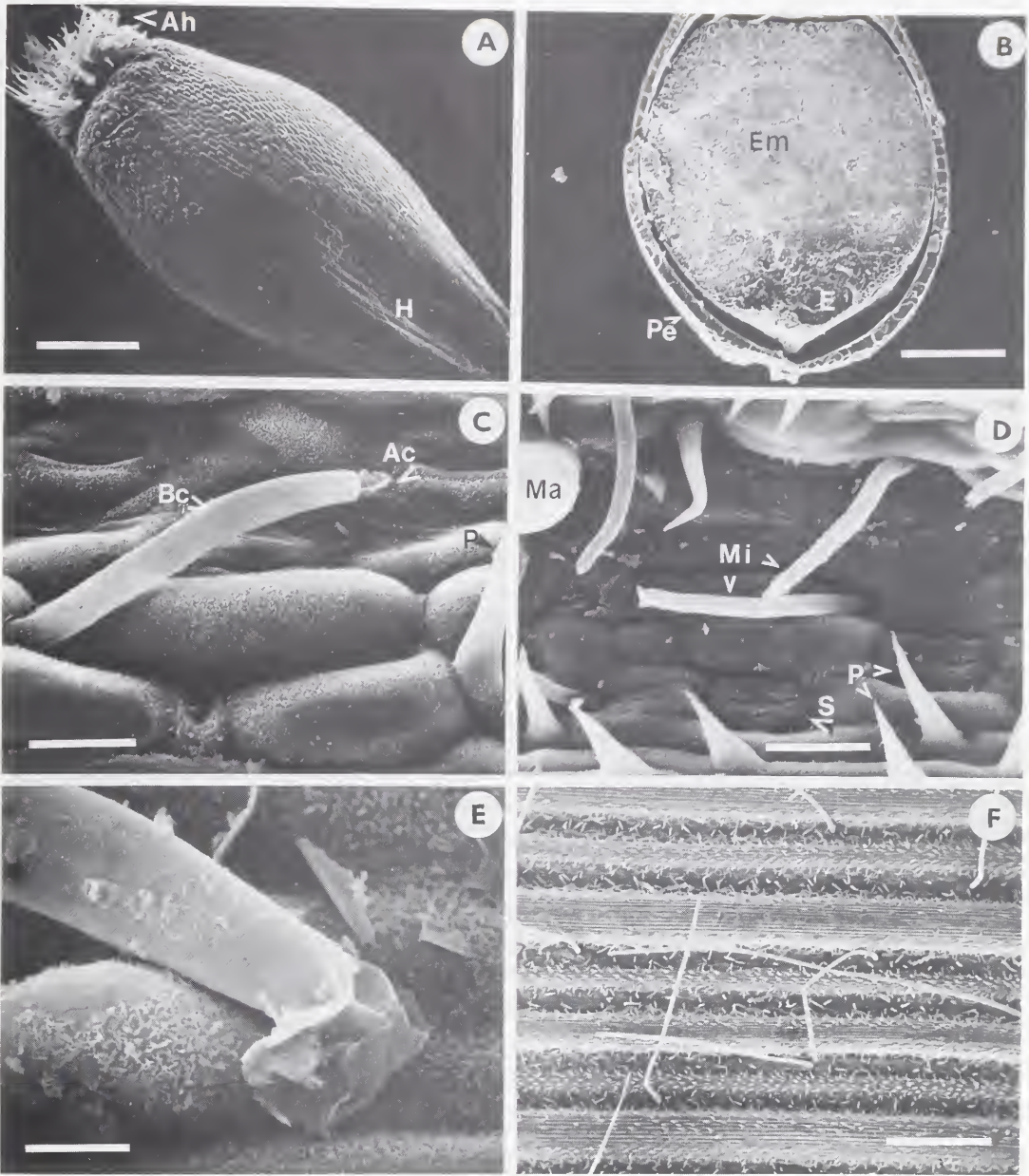


FIGURE 1. —*Pentameris*: A, B, SEM of fruit; C–F, SEM of leaf blade. A, *P. hirtiglumis* N.P. Barker, whole fruit, note colliculate surface features and apical hairs. B, D, F, *P. thuarii* Beauv.: B, longitudinal section; D, furrow on adaxial surface; F, adaxial surface showing ribs over vascular bundles and open furrows between ribs. Note abundance of conventional macrohairs and slightly inclined, sparsely distributed prickles. C, *P. distichophylla* (Lehm.) Nees, adaxial microhair. E, *P. oreophila* N.P. Barker, magnified view of deflated apical cell of adaxial microhair. Ac, small deflated apical cell; Ah, apical hairs; Bc, long basal cell; E, embryo; Em, endosperm; H, hilum; Ma, macrohair, basal portion; Mi, microhair; P, prickles; Pe, free crustaceous pericarp, seed within; S, stomata. Scale bars: A, 390 μ m; B, 541 μ m; C, 19 μ m; D, 33 μ m; E, 6 μ m; F, 550 μ m.

Scanning electron microscope (SEM) studies on the fruit of *Pentameris* have shown the pericarp to be sculptured (Barker 1986, 1989, 1990) as illustrated here in Figure 1A, and partly or almost completely free from the seed coat when viewed in section (Barker 1990) as shown here in Figure 1B. The colliculate surface sculpturing is also unique among the fruit of the southern African genera of the Arundineae (Barker in prep. b).

The second feature that characterises the genus is the presence of hairs on the apical region of the ovary and fruit. This was first observed by Palisot de Beauvois (1812), who described the fruit as being crowned with stellate hairs. Nees (1841) also noted this feature in his descriptions of *P. thuarii* and the taxon now known as *P. macrocalycina*. Phillips (1931) considered these hairs to be characteristic of the genus, using this feature in his

TABLE 1.—Salient anatomical characters differentiating the species of *Pentameris*. All measurements in micrometres

Character	<i>distichophylla</i>	<i>glacialis</i>	<i>hirtiglumis</i>	<i>longiglumis</i>	<i>macrocalycina</i>	<i>oreophila</i>	<i>swartbergensis</i>	<i>thuarii</i>	<i>uniflora</i>
Rib shape in T/S	1' & 3' squared	1' & 3' round	1' squared, 3' rounded	1' squared, 3' rounded	1' rounded, 3' conical	1' rounded, 3' conical	1' & 3' rounded	1' & 3' rounded	1' squared, 3' rounded
Relative depth of 1' and 3' ribs	1' = 3'	1' = 3'	1' > 3'	1' > 3'	1' > 3'	1' > 3'	1' = 3'	1' = 3'	1' = 3'
Leaf shape in T/S	rolled	rolled	rolled	'U'-shaped	acicular	permanently rolled	rolled	flat, 'V'-shaped or rolled	rolled
Depth of furrows between ribs	shallow	shallow	deep	deep	deep	deep	shallow	shallow	shallow
Width of furrows	narrow	wide	narrow	narrow	narrow	narrow	wide	wide	narrow
Shape and nature of abaxial 1' VB sclerenchyma girder	trapezoid and discrete	trapezoid and discrete	trapezoid, continuous with hypodermal band	trapezoid, continuous with hypodermal band	trapezoid, continuous with hypodermal band	trapezoid, continuous with hypodermal band	equidimensional, discrete	equidimensional—trapezoidal, discrete	trapezoid, discrete
Nature of sclerenchyma cap at leaf margin	poorly developed, discrete	poorly developed, discrete	well developed, continuous with hypodermal band	well developed, continuous with hypodermal band	poorly developed, continuous with hypodermal band	well developed, continuous with hypodermal band	poorly developed, discrete	poorly developed, discrete	poorly developed, continuous with hypodermal band
Nature of leaf blade near edges	unswollen	unswollen	swollen	swollen	unswollen	unswollen	unswollen	unswollen	unswollen
Abaxial epidermal cell width:									
mean	21.9	25	29.6	40.0	30.4	19.6	23.7	20.8	36.5
std. deviation	4.39	n/a	4.03	5.02	5.24	3.17	4.49	4.42	3.57
range	12–29	n/a	24–35	32–48	22–44	14–25	20–30	13–28	32–42
sample size	19	1	7	8	21	10	3	10	4
Mean blade width at midrib	201	171	250	345	366	301	166	231	165
std. deviation	250	n/a	28.7	47.5	57.1	48.4	16.5	29.6	5.6
range	142–236	n/a	200–289	274–444	307–506	185–385	153–189	188–282	156–171
sample size	19	1	7	8	21	10	3	10	4
Abaxial macro-hairs	sometimes present	sometimes present	sometimes present	absent	absent	absent	absent	absent	absent
Adaxial macro-hair presence and type	conventional and filament types	conventional type	conventional type	filament type	filament type	filament type sometimes present	conventional and filament types	conventional type	filament type
Adaxial prickly type; structure; orientation and density	needle-like; knobbed; erect; sparse	inflated; erect with tips bent over; dense	inflated; with basal collar; appressed to surface; dense	inflated; appressed to surface; dense	inflated; tips curling over; erect; dense	long, needle-like; erect with tips bent over; collar; dense	inflated; erect with tips bent over; sparse	inflated; erect with tips slightly bent; sparse	inflated; erect with tips slightly bent; dense
Adaxial prickly length	33	32–39	52–64	79–83	44	122	32–39	37–45	44
Mean adaxial micro-hair length	72	95.7	122	142	109	105	88	71	45
ranges	68–76	71–116	105–145	129–156	101–118	103–108	75–101	68–75	45
sample size	5	4	3	3	2	2	2	3	1

1' = primary vascular bundles; 3' = tertiary vascular bundles.

key to the grass genera. Chippindall (1955) describes *Pentameris* as having an ovary which is hairy on top, the hairs being deciduous. This character was also used in the key to the genera of the tribe Danthonieae. The nature of these unusual structures has been clarified to a certain extent by Barker (1986, 1989, 1990), but their ontogeny and function is not known. These structures, visible on the apex of the fruit (Figure 1A) appear to be unicellular, and arise from the apex of the ovule around the base of the styles.

LEAF BLADE ANATOMY

Leaf blade anatomy has contributed much to the tribal and subfamilial classification of the grass family. However, within the tribe Arundineae, the variation of observed anatomical characters led Renvoize (1981) to comment that the arundinoid genera could not be readily divided into the tribal groups on the basis of their leaf anatomy, and he concluded that other characters such as spikelet morphology would have to be used to divide the subfamily further.

The leaf blade anatomy of many of the southern African arundinoid genera has been documented (Schweickerdt 1942; De Wet 1956; Conert & Tuerpe 1969; Ellis 1980; 1981; 1985a–d).

Ellis (1985a–d, 1986) examined many specimens of the then five known and one undescribed species of *Pentameris*. Additional anatomical information for the new and undersampled species was obtained by sectioning a small portion of leaf material obtained from herbarium specimens. This material was heated in a soapy solution prior to sectioning by means of a sledge microtome. Sections thus obtained were 30 to 50 microns thick. The sections were stained in safranin and fast green and mounted in Euparal.

To complement the data obtained from the work of Ellis (1985a–d, 1986) and additional sections, leaf material from 95 of these previously studied specimens was prepared from herbarium specimens, mounted on two-sided tape, coated in gold-palladium and examined using a ISI-SX-25 scanning electron microscope. The salient anatomical features obtained from the SEM and light microscope studies are presented in Table 1.

The abaxial surface is relatively uniform throughout the genus. It is generally smooth, with ribs observed only occasionally. No abaxial microhairs or stomata are present, and the silica bodies are usually rounded, but are tall and narrow in *P. thurarii* (Ellis 1985b–d, 1986). Abaxial macrohairs were occasionally present in specimens of some taxa (Table 1). The adaxial epidermis is far better endowed with micromorphological structures, including prickles, microhairs and macrohairs. These epidermal features are discussed in some detail below.

Microhairs

The genus *Pentameris* has a 'festucoid' type of leaf epidermis and leaf anatomy (implying the absence of abaxial microhairs), a poorly differentiated parenchyma sheath and evenly distributed chlorenchyma sheath (De Wet 1956). However, Renvoize (1986) places *Pentameris*

in the 'core' of the arundinoids, a group possessing microhairs, and describes the lower epidermis of *Pentameris* and *Pseudopentameris* as possessing long slender papillae which occasionally bear the remains of a small thin-walled apical cell. Clayton & Renvoize (1986) note that these structures distinguish these genera (and certain others such as *Cortaderia* Stapf and *Centropodia* Reichb. f.) from the rest of the Arundineae.

These 'papillae', as described by Renvoize (1986) and Clayton & Renvoize (1986), appear to differ from those described by Ellis (1979), who considers papillae to be protuberances of the cell wall rather than structures consisting of separate cells. From observations discussed below, it appears that Renvoize is using the term 'papillae' to describe what others, such as De Wet (1956) and Ellis (1979), call microhairs.

In addition to their structure and appellation, the recorded distribution of these microhairs is also controversial. Renvoize (1986, discussed above) reported them from the lower (abaxial) surface of specimens of *Pentameris*. However, Ellis (1985a–d, 1986) has found no evidence of abaxial microhairs on any of the specimens he has examined. Microhairs were however found on the sides and bottoms of the furrows of the adaxial surfaces of many specimens in all the taxa observed (Ellis l.c.). My observations on material examined, using the SEM, corroborate Ellis's observations, and it is clear that there are no abaxial microhairs present in any of the species of *Pentameris*.

As illustrated in Figure 1C, D and E, these microhairs are indeed bicellular, with a minute, deflated apical cell (shown at high magnification in Figure 1E). The length of the basal cell varies, but it is always very much longer than the apical cell. Microhairs with this structure were found on the adaxial surface of all specimens of all taxa in *Pentameris* (Barker 1990), and were also reported from certain species of *Pentaschistis* (Ellis & Linder 1992).

In addition to their distribution and morphology, variation in the size of the microhairs is taxonomically useful. The microhairs were measured from a number of SEM micrographs in order to determine whether or not there was any measurable size difference. These varying sizes are recorded in Table 1. Unfortunately, the limited sample size does not allow a statistically meaningful comparison to be carried out on this potentially very valuable taxonomic character.

The definite bicellular nature of these microhairs is comparable to those reported and illustrated by Amarasinghe & Watson (1988, 1989). However, microhairs with such unequal cell sizes have not been previously documented, and perhaps merit recognition as a separate type of microhair, the 'pentameroid' type.

Abaxial macrohairs

Abaxial macrohairs were only observed on the abaxial surface of some specimens of *Pentameris distichophylla*, *P. hirtiglumis* and *P. glacialis*. In all these taxa, the hairs were long, usually produced from the intercostal regions, had a distinctly swollen base and were surrounded by four or more cells, termed 'modified cells' by Ellis (1986). The taxonomic value of these structures is limited, as it

appears that they are not universally present throughout all specimens examined of all taxa. Inconsistent sampling (variation in the region of the leaf from which the samples were taken, or the age of the leaf blade) may explain the lack of macrohairs in some samples.

Adaxial macrohairs

Two different hair-like structures were found on the adaxial leaf surface in some of the taxa of *Pentameris*, sometimes both occurring on the same leaf. Conventional macrohairs, those which have a distinct basal structure comprised of modified cells, were frequently observed on the adaxial epidermis in *Pentameris thuarii*, *P. glacialis* and *P. distichophylla*, but were only occasional in *P. swartbergensis*. Figure 1F illustrates these hairs on the adaxial leaf blade surface in *P. thuarii*.

The second type of macrohair, termed here a 'filament', is a long, unicellular hair without any obvious basal differentiation or associated cells. Although no measurements were taken, the filament type of macrohair appeared to be shorter than the conventional type. Filaments were frequently observed in the bottom of the adaxial furrows in specimens of *P. macrocalycina* and occasionally in *P. distichophylla* and *P. swartbergensis*. In *P. oreophila*

filaments were only found in the furrow nearest the edge of the lamina. One of these filaments observed in *P. distichophylla* is shown in Figure 2A.

Adaxial macrohairs are of slightly greater taxonomic significance than abaxial macrohairs. The presence and type of macrohair are useful characters in *Pentameris*, although some variability within the species exists. It appears that the species with open or folded leaves (*P. thuarii*, *P. distichophylla* and *P. swartbergensis*) possess conventional macrohairs, whereas those taxa with permanently rolled or folded leaf blades have the second type of macrohair (*P. macrocalycina*, *P. oreophila*, *P. distichophylla* and *P. swartbergensis*). *P. swartbergensis* and *P. distichophylla* thus have both types of macrohair. It is possible that the filament macrohairs are conventional macrohairs that have lost the modified cells around the hair base. The loss of these modified cells may be related to the evolution of the permanently rolled leaf blade, where the adaxial surface is not as exposed to the environment.

Prickles

The adaxial surfaces of all the specimens examined had prickles of one form or another. These different prickles types (Table 1) are invariant within the taxa of the genus.

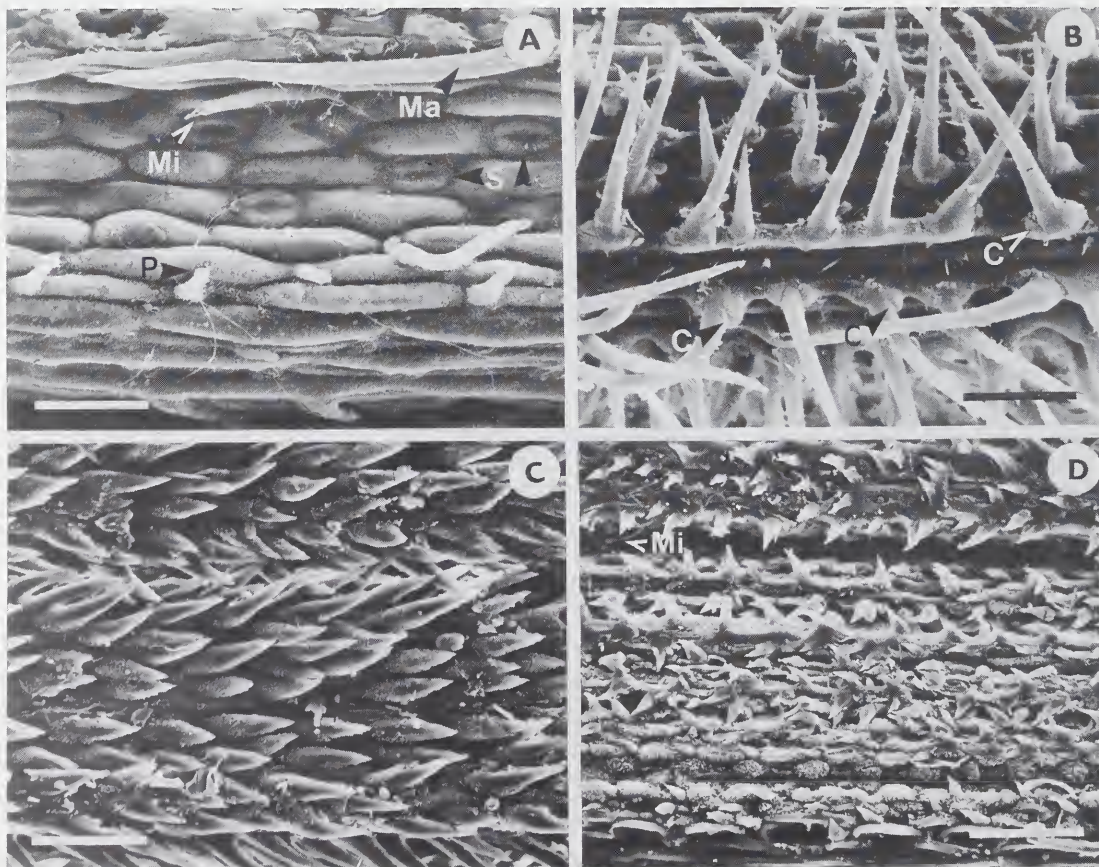


FIGURE 2.—Leaf blade SEM of *Pentameris*. A, *P. distichophylla* (Lehm.) Nees, adaxial surface; B, *P. oreophila* N.P. Barker, adaxial surface, note extreme length of prickles and presence of collar at base of each prickle; C, *P. longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker, adaxial surface, note extreme density and inclination of prickles; D, *P. uniflora* N.P. Barker, adaxial surface showing prickles and small microhairs. C, collar; P, prickles; Ma, macrohairs; Mi, microhairs; S, stomata. Scale bars: A, 48 μ m; B, 50 μ m; C, 87 μ m; D, 120 μ m.

Characters such as prickles density, distribution, orientation, length and structural differences are all taxonomically useful for distinguishing taxa within *Pentameris* (Figure 2A–D).

The prickles of *P. oreophila* are long and erect, with the tips sometimes bent or recurved. In addition to their unusual length, the prickles possess a basal collar-like structure (Figure 2B), a character shared with *P. hirtiglumis*. The prickles of the latter species are, however, much shorter, and are almost appressed to the surface of the leaf, a character shared with *P. longiglumis* (Figure 2C).

Of the remaining species, *P. macrocalycina*, *P. thuarii*, *P. glacialis* and *P. swartbergensis* have short, erect prickles, the tips of which may be bent or curved; are swollen basally, and the sides are convexly shaped; are densely distributed, particularly so in *P. macrocalycina*. The prickles of *P. uniflora* are also quite densely distributed and almost erect, as indicated in Figure 2D.

In contrast to the above, *P. distichophylla* has erect prickles that are almost straight-sided (as opposed to the slightly inflated convex sides of the prickles of the other taxa); they appear to have knobbed tips (Figure 2A) and are sparsely distributed over the adaxial surface, usually only on the edges of the ribs. Both the short, inflated prickle type and the erect, knobbed prickle type have also been observed in species of *Pentaschistis*, for example *P. colorata* (Ellis & Linder 1992). The long, collared prickles observed in *P. oreophila* are unique among the African Arundineae.

CYTOLOGY

Preliminary cytological studies have shown that *Pentameris distichophylla* has a chromosome count of $2n=36$, whereas *P. thuarii* has a count of $2n=12$. The latter figure has been corroborated by H. du Plessis (pers. comm.). Both these counts were obtained from meiotic material. *P. distichophylla* is therefore hexaploid. Such polyploidy is not unusual in the southern African Arundineae (see for example counts for *Merxmuellera*, *Pentaschistis* and other genera given by Du Plessis & Spies 1988; Spies & Du Plessis 1988; Spies *et al.* 1990).

These counts further support the contention that the base chromosome number for the Arundineae appears to be $x=6$ (Davidse 1988), and not $x=12$ as proposed by Clayton & Renvoize (1986). Despite the apparent similarities between *Pentameris* and *Pentaschistis*, the different base chromosome number of the latter genus ($x=7$ in many of the known instances) does not suggest a close relationship between these two taxa. It is, however, possible that *Pentameris* evolved by means of aneuploidy from a pentaschistoid ancestor.

PHYLOGENY

The data presented in Table 1 were converted into a data set suitable for cladistic analysis. The anatomical characters were augmented by a few morphological characters, resulting in a data set of 26 characters (presented in Tables 2 & 3). Four of these characters are

TABLE 2.—Characters used in the cladistic analysis. 1' = primary vascular bundles, 3' = tertiary vascular bundles

Leaf blade characters (t/s)

1. Leaf blade shape in t/s: 0 = flat to curled, 1 = rolled, 2 = permanently rolled
2. 1' rib shape: 0 = squared, 1 = round
3. 3' rib shape: 0 = squared, 1 = round, 2 = conical
4. Relative rib depth: 0 = 1' = 3'; 1 = 1' < 3'
5. Furrow depth: 0 = shallow (< 1/2 lamina thickness) 1 = deep
6. Furrow width: 0 = narrow, 1 = wide
7. 1' Abaxial sclerenchyma girder: 0 = discrete, 1 = continuous with hypodermis
8. Sclerenchyma cap on leaf margin: 0 = discrete, 1 = continuous with hypodermis
9. Leaf blade thickness: 0 = uniform thickness, 1 = swollen near margin
10. Abaxial epidermal cells: 0 = small (< 25 μ m wide), 1 = inflated
11. Silica body shape: 0 = round, 1 = dumbbell-shaped

Adaxial epidermal characters

12. Conventional macrohair type: 0 = absent, 1 = present
13. Filament macrohair type: 0 = absent, 1 = present
14. Prickle type: 0 = inflated basally, 1 = markedly elongated, 2 = apically knobbed
15. Prickle orientation: 0 = erect, 1 = inclined/appressed
16. Prickle base: 0 = unornamented, 1 = collar present
17. Prickle density: 0 = sparse, 1 = dense
18. Microhair type: 0 = basal cell length >> apical cell length 1 = basal cell length = apical cell length
19. Microhair length: 0 = short (< 60 μ m), 1 = long
20. Papillae: 0 = absent, 1 = present

Morphological characters

21. Growth form: 0 = unbranched, 1 = branched
22. Glands: 0 = absent, 1 = present
23. Lodicule margin: 0 = entire, 1 = ciliate
24. Achene surface: 0 = rugose, 1 = colliculate, 2 = reticulate
25. Fruit type: 0 = caryopsis, 1 = achene
26. Ovary appendages: 0 = absent, 1 = present

multistate, and are treated as undirectional in the analysis. The 'ie' option of the cladistic package HENNIG86 version 1.5 was used to analyse the data. Using this method, the complete set of most parsimonious trees is found (Platnick 1989).

Choice of outgroup

Pentaschistis is the obvious outgroup, although the recognition of a particular species or group of species within this genus as the closest to the study group is not possible on an *a priori* basis. Six species of *Pentaschistis* were therefore chosen as possible outgroup taxa. These taxa were chosen on the basis of inferences made by Ellis in his anatomical papers (1985c, 1986), and after discussions with Dr H. P. Linder. The taxa chosen were *P. aspera* (Thunb.) Stapf, *P. colorata* (Steud.) Stapf, *P. curvifolia* (Schr.) Stapf, *P. eriostoma* (Nees) Stapf, *P. glandulosa* (Schr.) Linder and *P. tortuosa* (Trin.) Stapf.

Two of these taxa, the glandular *P. glandulosa* and *P. aspera*, were included because they were considered to be most dissimilar to the study group. Following the outgroup substitution method of Donoghue & Cantino (1984), these two least related glandular taxa were used as the initial outgroup to determine the relationships between the remaining taxa. Using this method, the single

TABLE 3.—Data used in cladistic analyses. Characters marked by asterisks above the data set were removed in the data set where *Pentastichis curvifolia* was used as the outgroup (data set delimited below the dashed line). Characters appear in the order presented above. The question mark (?) indicates absent data

	Characters																						26		
	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Pentastichis:</i>																									
<i>aspera</i>	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	2	0	0	0	0	
<i>glandulosa</i>	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0	0	1	0	2	0	0
<i>colorata</i>	1	0	0	1	0	0	0	0	1	1	0	1	2	0	0	0	1	0	1	?	0	1	2	0	0
<i>tortuosa</i>	1	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	2	0	0
<i>eriosoma</i>	1	0	2	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	1	2	0	0
<i>curvifolia</i>	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	2	0	0
<i>Pentameris:</i>																									
<i>distichophylla</i>	1	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0	0	1	0	1	0	1	1	1	1
<i>glacialis</i>	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	1	1
<i>hirtiglumis</i>	1	0	1	1	1	0	1	1	1	1	0	0	0	0	1	1	1	0	1	0	1	0	1	1	1
<i>longiglumis</i>	1	0	1	1	0	0	1	1	1	1	0	0	0	0	1	0	1	0	1	0	1	0	1	1	1
<i>macrocalycina</i>	2	1	2	1	1	0	1	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1
<i>oreophila</i>	2	1	2	1	1	0	1	1	0	0	0	1	1	0	1	1	0	1	0	1	0	1	1	1	1
<i>swartbergensis</i>	1	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	1	1	1
<i>thuarii</i>	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1
<i>uniflora</i>	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	?	1	1

or few non-study group taxa found to be most closely related to the study group were then used to perform the final cladistic analysis on the data set from which the other outgroup taxa had been removed.

When the two distantly related taxa are used as the outgroup, one shortest length tree (l. = 60, c.i. = 50, r.i. = 67) is generated. In this tree (not presented), *P. curvifolia* is the taxon most closely related to the study group, and was used as the outgroup (the other *Pentastichis* species were removed from the data set); the data were re-analysed after the autapomorphies and invariant characters had been removed. Once again, HENNIG86 found one shortest tree, presented in Figure 3 (l. = 34, c.i. = 64, r.i. = 70). The phylogeny of the study group in this tree is identical to that obtained in the initial tree (not presented) where the two glandular taxa are used as an outgroup.

Character distribution

In discussing the distribution of the characters on the tree, the characters from the complete database are used, although in the smaller data set (where *Pentastichis curvifolia* is the outgroup) some are excluded because they are constant or autapomorphic. The distribution of the characters is shown on this tree (Figure 3).

The genus *Pentameris* is a monophyletic clade supported by the ovule and fruit characters; the apical appendages and the achene fruit type (char. 25 and 26, represented by the star in Figure 3).

Within *Pentameris*, two smaller clades are recognised. The first clade comprising *P. distichophylla*, *P. thuarii*, *P. glacialis* and *P. swartbergensis* is supported by the presence of conventional macrohairs on the adaxial surface (char. 12). Within this group, *P. distichophylla* is basal to the other three taxa and is characterised by the autapomorphies of knobbed prickles (char. 14), the rounded ribs of the tertiary vascular bundles (char. 3) and the rugose pericarp surface (char. 24). *P. thuarii*, *P. glacialis* and

P. swartbergensis share a flat leaf blade with wide furrows between the adaxial ribs (char. 6). *P. glacialis* and *P. thuarii* share a character that has arisen in parallel elsewhere: entire lodicule margins (char. 23).

The other clade within the genus is supported by the presence of dense prickles (char. 17), as well as other characters which undergo reversals in some of the lower

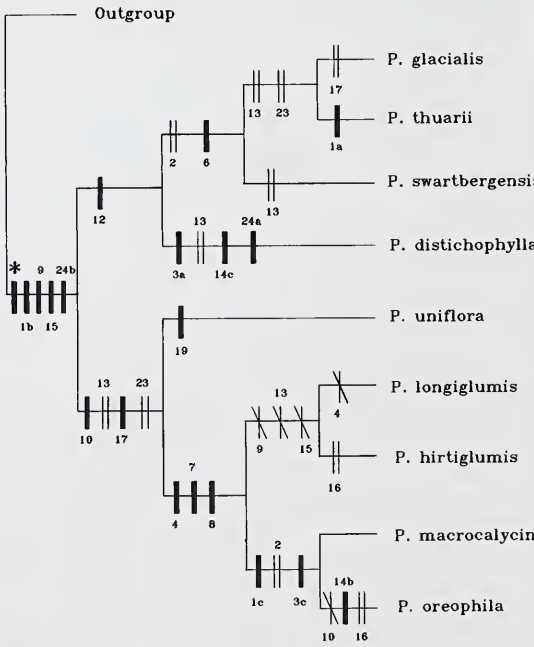


FIGURE 3.—Shortest cladogram produced by HENNIG86 using the 'ie' option. The outgroup used was *Pentastichis curvifolia* (Schr.) Stapf. Length = 34, c.i. = 64, r.i. = 70. Numbers represent characters (given in Tables 2 & 3; 'a' = state 0, 'b' = state 1 and 'c' = state 2). Solid bars represent apomorphies, parallel lines represent parallelisms and crosses represent character state reversals. Star at base of *Pentameris* clade represents apomorphic fruit characters: achene fruit type and presence of apical hairs on ovary.

clades (char. 10 and char. 13: abaxial epidermal cell width and presence of filament macrohairs respectively). *P. uniflora* is basal to this clade, characterised by the presence of one floret (data not included in data set) and short microhairs (char. 19). The remaining four taxa are united by the presence of a continuous hypodermal band of sclerenchyma which connects to the abaxial girders and cap on the leaf margin (char. 7 and 8), and primary ribs which are deeper than the tertiary ribs (char. 4). *P. longiglumis* and *P. hirtiglumis* both have enlarged or swollen leaf blade margins (char. 9), as does the outgroup. *P. macrocalycina* and *P. oreophila* share conical tertiary ribs (char. 3) and permanently rolled leaf blades (char. 1). The latter species is distinguished by the autapomorphy of long prickles (char. 14).

The low consistency index obtained from the analysis of the complete data set (c.i.=50) indicates the homoplasy present within the data set. This is further demonstrated by the increase in the value of the consistency index with the removal of all but the closest outgroup taxa (c.i.=64). Characters which are synapomorphies in the reduced data set are often homoplastic in the complete data set. For example, the unequal primary and tertiary vascular bundle thicknesses (char. 4) is a synapomorphic character for the *P. longiglumis*, *P. hirtiglumis*, *P. macrocalycina* and *P. oreophila* clade in the analysis based on the reduced data set. However, in the large data set, this character is also present in *Pentaschistis aspera*, *P. glandulosa*, *P. colorata* and *P. tortuosa*. Similar situations are found in other characters. Such homoplasy has probably been one of the root causes bedevilling the efforts of taxonomists, both past and present, to find an equitable classification for this group.

Taxonomic implications

The monophyletic status of *Pentameris* is supported by the fruit and ovary characters. However, as *Pentameris* is undoubtedly closely related to *Pentaschistis* (at least the eglandular taxa), the possibility that the latter genus is paraphyletic ought not to be ruled out. The observation that *Pentameris* was placed within, and terminal to, the *Pentaschistis* clade in the analysis of the complete data set provides some evidence as to this possibility. If this is the case, the name *Pentameris* would be retained for the monophyletic assemblage containing the taxa with the unique fruit characters, while other genera may have to be erected to accommodate monophyletic groups within the *Pentaschistis* assemblage. Only a detailed phylogenetic study of both *Pentaschistis* and *Pentameris* can provide sufficient data to properly test any hypothesis of parphyly.

CONSERVATION STATUS

Of the previously known taxa of *Pentameris*, only *P. obtusifolia* is listed in the Red Data Book as a rare, threatened or extinct species, where it is listed under the synonym '*P. squarrosa*' (Hall & Veldhuis 1985). The conservation status for this taxon is given as 'uncertain'. However, as discussed above, the nomenclature of this taxon has been found to be confused, and *P. obtusifolia* is not included in the genus *Pentameris*.

Certain species of *Pentameris* nonetheless require consideration and recognition as taxa requiring conservation. Most of the new taxa described below are known from only a few localities, and should perhaps be regarded as 'rare'. However, as many of these taxa are found in inaccessible and thus rarely collected areas, the true distribution is not fully known. In addition to the problem of varying collecting intensity, the effects of fire on the germination, growth and re-establishment of fynbos grass species are poorly known. Linder & Ellis (1990a) discuss the various strategies that fynbos grasses have evolved to escape or adapt to fire. These authors note that grasses appear in abundance in the first few years after fire, but are then almost inevitably outcompeted by members of the Restionaceae and woody fynbos elements. The collection of fynbos grasses is therefore best carried out in areas that have been burnt within the previous few years. Such areas are not always attractive to collectors intent on obtaining other woody or non-graminoid taxa. Mature, woody fynbos may therefore hide many new or apparently rare grass species which are present as dormant seeds or underground vegetative structures. Actual species distributions may therefore be wider than presently known.

In assessing conservation status of the taxa of *Pentameris*, the categories proposed by Rabinowitz (1981) and modified by Karron (1987) will be used. These categories record the geographic distribution, demographic structure and habitat requirements in a two-state form: restricted or widespread, sparse or abundant, wide or narrow respectively. The demographic component can thus reflect, to a certain extent, the biological aspects of rarity of the taxa.

As the category of geographic distribution is scale dependent, it is used here at the level of magisterial districts or mountain ranges, whichever is more geographically homogeneous. The allocations of the species of *Pentameris* to these categories is presented in Table 4. Detailed descriptions of distributions and habitats are provided under individual species descriptions.

TAXONOMY

Taxonomic descriptions of all the taxa are presented. The dimensions given below for the lemma body, lemma

TABLE 4.—The modified Rabinowitz conservation categories allocated to each taxon of *Pentameris*. The allocation of these codes is based on field observations and data obtained from labels on herbarium specimens

<i>Pentameris</i>	Geographic distribution	Demographic structure	Habitat requirements
<i>distichophylla</i>	WS	A	W
<i>glacialis</i>	R	A	N
<i>hirtiglumis</i>	R	A	N
<i>longiglumis</i>			
subsp. <i>gymnocolea</i>	R	S	N
subsp. <i>longiglumis</i>	R	S	N
<i>macrocalycina</i>	WS	A	W
<i>oreophila</i>	WS	A	N
<i>swartbergensis</i>	R	A	N
<i>thuaria</i>	WS	A	N
<i>uniflora</i>	WS	A	N

A = abundant; N = narrow; R = restricted; S = sparse; W = wide; WS = widespread.

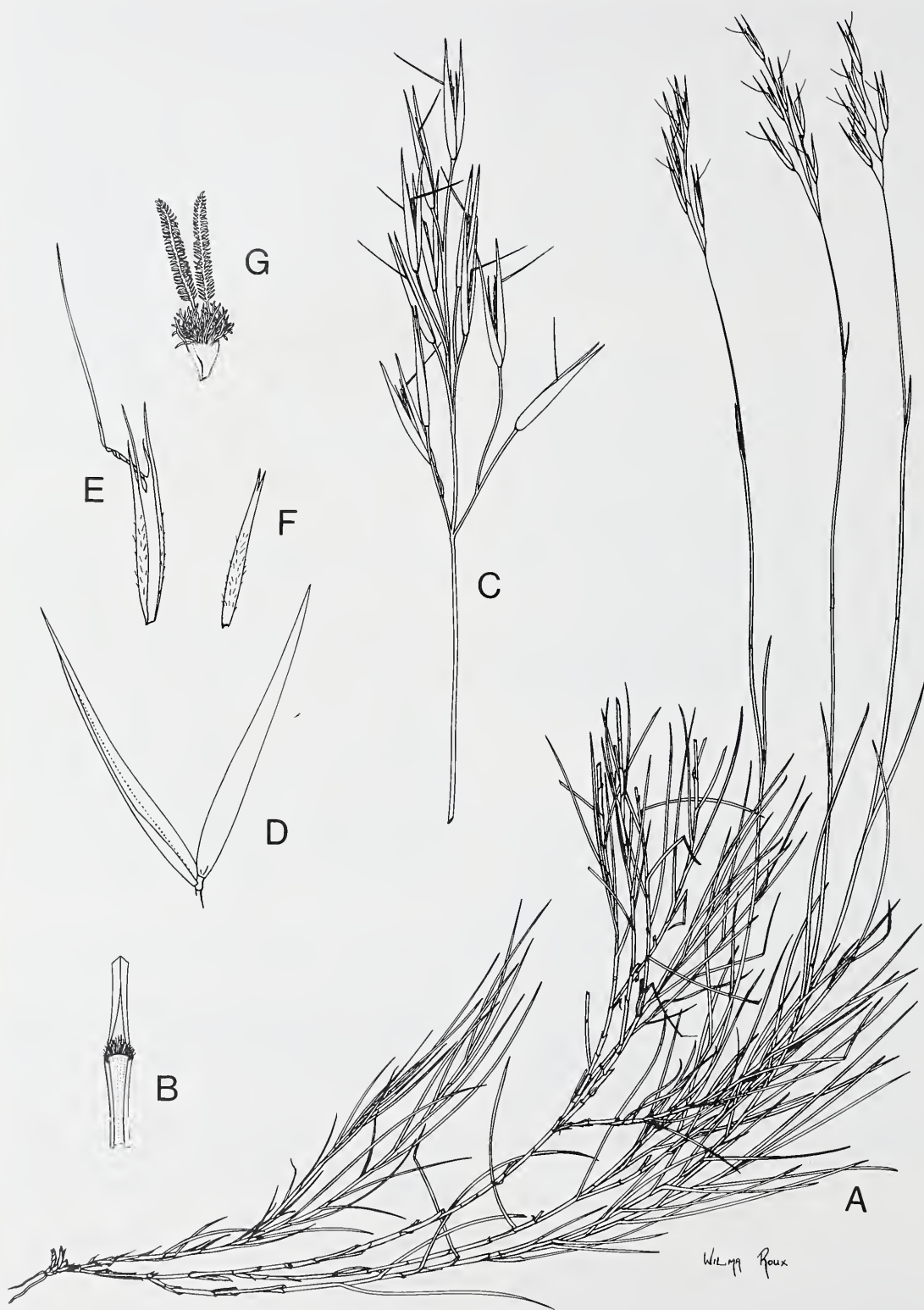


FIGURE 4.—*Pentameris uniflora* N.P. Barker. A, habit with decumbent, branching culm basally covered in dead, appressed leaf sheaths; B, ligule, which is a row of hairs, and surrounding leaf parts; C, panicle subcontracted to lax, with few spikelets. D–G, parts of spikelet and florets: D, glumes; E, lemma (in its normal conformation) showing lemma bristles, lobes (which are adnate to the bristle for most of their length) and geniculate awn; F, palea; G, ovary with apical hairs and stigmas. A, $\times 0.5$; B, D–F, $\times 4.7$; C, $\times 1.6$; G, $\times 11.8$.

lobes and lateral bristles are measured as follows: the lemma body is measured from the base to the lowermost point of insertion of the central awn, whereas the lobes and bristles are measured from this same insertion point to the apex of the lobe or bristle. The full length of the lemma (either from base to lobe apex or base to bristle tip) can be obtained by adding the lemma body length to the length of the lobe or bristle. The term 'culm' is used in the descriptions below to describe all aerial parts (branched stems and reproductive culms) despite the anatomical discrepancies discussed in the introduction.

Pentameris Beauv., Essai d'une Nouvelle Agrostographie: 92, t.18, fig.8 (1812); Kunth: 107 (1829); Kunth: 315 (1833); Nees: 336 (1841); Stapf: 512 (1897); Chippindall: 251 (1955); Clayton & Renvoize: 174 (1986); Gibbs Russell *et al.*: 251 (1990). Type species: *Pentameris thuarii* Beauv.

Perennial; caespitose, cushion-like or decumbent, sometimes branched. Culms 250–2 000 mm in length; woody and persistent from a woody base; leaf sheaths appressed to culm or free, persistent; sheath mouth sometimes auriculate; ligule a fringe of hairs; leaf blades linear, 50–550

mm long, rigid or filiform, open and flat, rolled or acicular; inflorescence paniculate, lanceolate and somewhat contracted to globose and lax; spikelets solitary, 13–25 mm long, laterally compressed, 1–2-flowered, highly reduced third floret rarely present; glumes two, more or less equal, 1-nerved, membranous to chartaceous, minutely scabrid, sometimes hirsute; lemma body uniformly pubescent, 7–9(–11)-nerved, 2.2–6.0 mm long, pubescent, the hairs arising from between the nerves, nerves anastomosing into the awn base and a 2.5–12.0 mm long lateral bristle; lemma lobes 0.4–4.0 mm long, acute to acuminate, sometimes lacerated, partly to fully adnate to the bristles; central awn geniculate, scabrid, contorted basally, 2–11 mm long from base to knee, 6–21 mm long from knee to tip; palea longer than lemma body, bifid at apex, pubescent between the keels; lodicules two, glabrous or ciliolate, sometimes with arm-like extensions; stamens three; ovary apically hairy, these hairs retained until maturity; fruit an achene with free pericarp, fusiform, subglobose to globose or cuneate, surface colliculate or rugose, hilum up to two thirds the length of the fruit, embryo small.

A genus of nine species, endemic to the southwestern region of the Cape Province, South Africa.

Key to species

- 1a Spikelets with one floret 1. *P. uniflora*
- 1b Spikelets with two florets, occasionally with a rudimentary third floret:
 - 2a Leaves with purple to dark brown auricles at base of blade; lemma lobes truncate, apically dentate .. 2. *P. thuarii*
 - 2b Leaves without auricles, or if present then not coloured as above; lemma lobes acute to acuminate:
 - 3a Panicle lax at anthesis, globose, 170–300 mm long; basal leaf sheaths 120 mm or longer, clustered at, and free from culm base; culm, including inflorescence, usually taller than 1.2 m:
 - 4a Leaf sheaths densely covered in short hairs; glumes 15–18 mm long; lemma body 3.0–3.5 mm long; known only from Table Mountain 3a. *P. longiglumis* subsp. *longiglumis*
 - 4b Leaf sheaths glabrous; glumes 21–24 mm long; lemma body 5.0–5.5 mm long; known only from the Kogelberg 3b. *P. longiglumis* subsp. *gymnocolea*
 - 3b Panicle subcontracted to contracted at anthesis, lanceolate, up to 150 mm long; basal leaf sheaths seldom longer than 120 mm, partially free or appressed to culm; culm, including inflorescence, seldom taller than 1.2 m:
 - 5a Glumes 14–24 mm long; leaf blades acicular or permanently rolled, rigid, sometimes pungent:
 - 6a One or both glumes pubescent 4. *P. hirtiglumis*
 - 6b Glumes never pubescent:
 - 7a Leaf blades acicular, usually straight but sometimes curling toward apices, occasionally pungent; leaf sheaths glabrous, but sheath mouth may be bearded; sheaths closely appressed to culm .. 5. *P. macrocalycina*
 - 7b Leaf blades permanently rolled, usually falcate, strongly pungent; leaf sheaths not appressed to culm, always pubescent, if only at margins 6. *P. oreophila*
 - 5b Glumes usually 14 mm or shorter; leaf blades usually soft, rolled (not permanently), folded or flat in cross section, never pungent:
 - 8a Lateral bristle of lemma 5.5–10.0 mm long; leaf sheaths pubescent to densely woolly, especially near sheath mouth 7. *P. distichophylla*
 - 8b Lateral bristle of lemma 2.5–5.5 mm long; leaf sheaths glabrous or pubescent at margin only:
 - 9a Leaves 200 mm long or longer, up to 5 mm wide; panicle with 25 or more spikelets 8. *P. swartbergensis*
 - 9b Leaves usually shorter than 100 mm, thin and rolled, narrower than 2 mm; panicle with fewer than 15 spikelets 9. *P. glacialis*

1. *Pentameris uniflora* N.P. Barker, sp. nov.

A aliis omnibus speciebus *Pentameridis* flosculo singulari differt.

Pentameris sp. 2. in Gibbs Russell *et al.*: 253 (1990).

TYPE.—Cape, Riversdale, Sleeping Beauty Peak. Along edges of overgrown ledges or on steep south slopes. Dense. 4200ft (1 275 m), 29 Oct. 1967, Esterhuysen 31771 (PRE, holo.!; BOL, iso.!).

Plants soft, decumbent; culms thin and flexuous, up to

650 mm long; leaf sheaths glabrous or only pubescent along margins, appressed to culm; leaf blades soft, filiform, short, up to 125 mm long, open or folded to somewhat rolled; panicle lanceolate, delicate, 40–60 × 10–20 mm, lax; spikelets 5–20, one-flowered; glumes 11–12 × 0.9–1.0 mm; lemma body 5.5–6.0 mm long; lemma lobes acuminate, 1.5–3.0 mm long, adnate to 2.5–4.5 mm long lateral bristle for most of their length; awn geniculate, 2.0–3.5 mm from base to knee, 6.5–7.0 mm from knee to tip; palea 5.5–6.0 mm long; lodicules cuneate, glabrous; anthers 4 mm long; fruit not known; flowering time September to December. Figures 2D; 4.

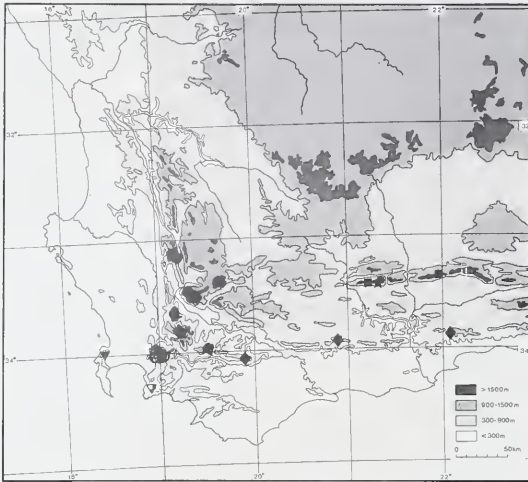


FIGURE 5.—Distribution of *P. glacialis* N.P. Barker, ■; *P. hirtiglumis* N.P. Barker, ○; *P. longiglumis* (Nees) Stapf subsp. *longiglumis* N.P. Barker, ▼; *P. longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker, ▽; *P. oreophila* N.P. Barker, ●; *P. swartbergensis* N.P. Barker, *; *P. uniflora* N.P. Barker, ◆; neighbouring locality of *P. hirtiglumis* and *P. oreophila*, ○.

This species is the only taxon in the genus with one-flowered spikelets. Mature fruit have not been seen, but stylar hairs on the apex of the ovary confirm the position of this species in the genus *Pentameris* (Barker 1990).

P. uniflora is known from only three localities which are quite widely separated (Figure 5). Populations at these localities appear to be quite abundant, but the habitat of this species (damp, rocky, southern aspects of the Cape fold mountains), habit (decumbent, hidden under taller plants), and small, somewhat inconspicuous inflorescences may account for the paucity of herbarium specimens.

Vouchers: Bond 1581 (SAAS); Ellis 2546 (PRE); Esterhuysen 25025, 32718a (BOL); Esterhuysen 31771 (BOL, PRE).

2. *Pentameris thuarii* Beauv., Essai d'une Nouvelle Agrostographie: 92, t. 18, fig. 8 (1812); Roem. & Schult.: 693 (1817); Kunth: 107 (1829) as 'thouarsii'; Kunth: 315 (1833) as 'thouarsii'; Kunth: 270 (1835) as 'thouarsii'; Stapf: 513 (1897); N.P. Barker in Gibbs Russell *et al.*: 253. (1990). Type: *Du Petit-Thouars s.n.* (P, lecto!). Lectotype here designated.

Danthonia thuarii Desv.: 99 (1831); Nees: 337 (1841) as 'thouarsii'; Steudel: 243 (1855) as 'thouarsii'; Durand & Schinz: 854 (1895) as 'thouarsii'; Durand & Schinz: 854 (1895).

P. thuarii Beauv. var. *burchellii* Stapf: 513 (1897). Type: Riversdale Div., lower part of the Lange Bergen, near Kampsche Berg, *Burchell* 6964 (K, holo!; GRA, iso!; PRE (fragment), iso!).

Plants caespitose or decumbent; culms 0.46–1.63 m long; leaf sheaths pubescent, appressed to culm, with purple auricle at mouth, persistent; leaf blades up to 500 mm long, folded or flat (rarely rolled); panicle globose, lax, 70–220 × 40–170 mm; spikelets 16–90, two-flowered; glumes 15.5–21.5 × 1.8–3.0 mm; lemma body 2.2–3.3 mm long; lemma lobes 0.4–0.7 mm long, acute, apically lacerate-dentate, almost free from a 4.0–5.5 mm

long lateral bristle; awn geniculate, 4.5–7.0 mm from base to knee, 9.5–12.5 mm from knee to tip; palea 2.8–3.5 mm long; lodicules cuneate, glabrous; anthers 3–4 mm long; fruit an achene, globose, 2.5 × 1.7–2.0 mm, surface colliculately sculptured; flowering time September to December. Figure 1B, D, F.

The spelling of the epithet *thuarii*, as used in the protologue, differs so obviously from that of the name of the collector, Du Petit-Thouars, that it is not considered a typographic error. The epithet *thouarsii*, used in a number of subsequent accounts, is therefore not adopted. It is plausible that Palisot de Beauvois wished to maintain the phonetic pronunciation of the French name 'Thouars', and thus spelt it 'thuarii' in latinised form.

No locality or specimen number of the type specimen was cited by Palisot de Beauvois. However, two specimens of *P. thuarii* were obtained from the Paris herbarium (P). One of these specimens is annotated with 'Herb. Du Petit Thouars', which is written on the bottom of the label. The identity of the handwriting is not known. That one (or both) of these specimens are type material is further supported by the observation that the illustration accompanying the original description includes a representation of a mature fruit, a description of which also appears in the text (Palisot de Beauvois 1812). The type specimen must therefore have borne mature fruit. This deduction is compatible with the historical record which indicates that Du Petit Thouars visited the Cape in February 1793. February is the time of year when many fynbos grasses, including *P. thuarii*, are in fruit (pers. obs.). As the annotated specimen from Paris is in full fruit, this specimen is regarded as type material. However, this evidence is considered to be insufficient to warrant holotype status for this specimen, which is therefore selected as a lectotype.

Stapf (1897) distinguished two varieties of *P. thuarii*: var. *thuarii*, was described as being only 1–2 ft. (300–600 mm) tall with a woody, sometimes branched, suffrutescent base, with leaves only 1 lin. (approximately 2 mm) wide and with a lax, open or contracted panicle; var. *burchellii* Stapf was considered to be taller, simple basally

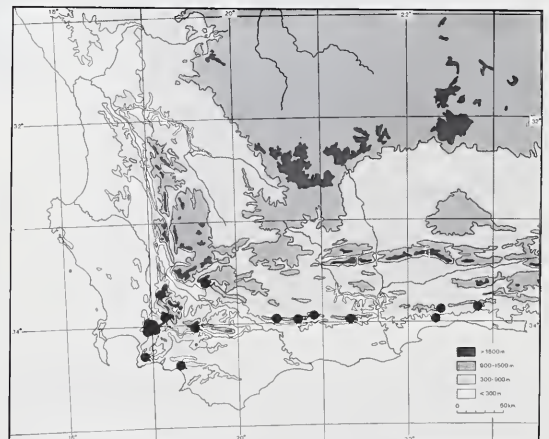


FIGURE 6.—Distribution of *P. thuarii* Beauv.

and branching after 1 ft. (300 mm), with leaves 2 lin. (approximately 4–5 mm) wide and with an effuse panicle. Stapf added that this latter variety has the appearance of a robust annual. Chippindall (1955) considers the characters on which these distinctions are made to be too variable, and rejects the two varieties, a conclusion supported by Barker (1990).

This species grows abundantly in moist environments, and is usually found alongside streams, seeps and drainage lines. Geographically widespread, it occurs from Stellenbosch in the west to Montagu Pass in the east (Figure 6).

Vouchers: *Ellis 2221* (PRE); *Compton 7494* (BOL, NBG); *Levyns 693* (BOL, STE); *Parker 4465* (BOL, NBG, SAM); *Schlechter 9282* (BOL, GRA, PRE).

3. *Pentameris longiglumis* (Nees) Stapf

The following description is based on all the specimens seen, and the variation reported includes that for both known subspecies, described below.

Plants densely tufted from a woody base; culms erect, up to 1.4 m tall, unbranched or branched close to woody base; leaf sheaths loose and free from culm, wide, persistent, clustered at base of plant, shortly pubescent or glabrous, straw-coloured or purple, sheath mouth sometimes with green auricles; leaf blades rigid, rolled, up to 550 mm long; panicle lax, globose, up to 300 × 140 mm; spikelets 30–100 or more, two-flowered; glumes 15.0–24.0 × 1.1–2.4 mm; lemma body 3.0–5.5 mm long; lemma lobes 2.4–4.0 mm long, long-acuminate, almost completely adnate to a 3.5–11.0 mm long lateral bristle; awn geniculate, 3.5–10.0 mm from base to knee, 7.5–21.0 mm from knee to tip; palea 3.0–9.5 mm long; lodicules cuneate, glabrous; anthers 3.6–5.5 mm long; fruit broadly fusiform, 3.5 × 1.3 mm, surface colliculately sculptured; flowering time September to December. Figures 8 & 9.

Two subspecies are recognised on the basis of a number of floral and vegetative characters, as listed in Table 5. The significance of these differences is demonstrated by the results of a principal components analysis (PCA)

TABLE 5.—A statistical summary of the variation in characters differentiating the two subspecies of *P. longiglumis* (Nees) Stapf. Measurements in mm

Character	subsp. <i>longiglumis</i>	subsp. <i>gymnocolea</i>
Sheath indumentum	pubescent	glabrous
Panicle dimensions	170 × 105	300 × 140
No. of spikelets	30–95	70–100
Glume length	15.0–19.5	21–24
Lemma body length	2.7–3.5	5.0–5.5
Lemma lobe length	2.4–3.0	3.5–4.0
Bristle length	3.5–8.0	8–11
Awn length:		
base to knee	3.5–5.0	8–10
knee to tip	7.5–10.0	14–21
Palea length	5.5–6.5	7.5–9.5

carried out on data obtained for 11 characters from 10 herbarium specimens. The PCA was done using the numerical taxonomy package NT-SYS, version 1.4 (Rohlf 1988).

The first three axes resulting from the PCA accounted for 94.2% of the variation in the data, with the first axis contributing 75.7%. The first two axes (Figure 7) account for 88.3% of the variation in the data. The two groups comprise specimens from two geographically distinct localities, Kogelberg and Table Mountain. On the basis of this evidence, the allocation of the rank of subspecies to these two groups is considered to be justified.

3a. *Pentameris longiglumis* (Nees) Stapf subsp. *longiglumis*

Danthonia longiglumis Nees in *Flora africae australioris* 1: 306 (1841).

TYPE.—Cape, In summo monte tabulare (Dist. Cap.), *Bergius s.n.* (B, holo.!; fragment and photo in PRE, iso!).

Note: *Pentameris longiglumis sensu* Stapf: 514 agrees with neither Nees's description nor the type (see discussion below).

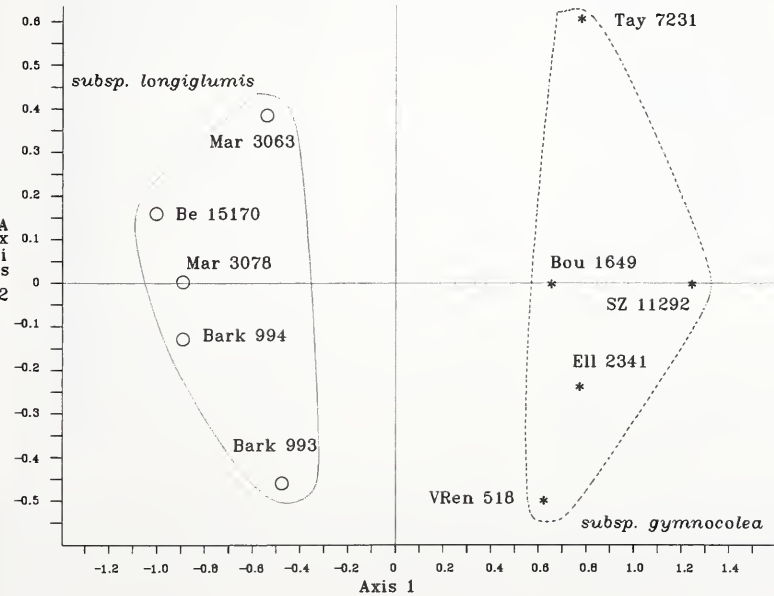


FIGURE 7.—First two axes of the principal components analysis on data of eight specimens of *Pentameris longiglumis* (Nees) Stapf. Axis 1 accounts for 75.7% of variation in data, axis 2, 12.6%. Points represent specimens, annotated as follows: Bark = Barker, Be = Bews, Ell = Ellis, Mar = Marloth, SZ = Stirton & Zantovska, Tay = Taylor, VanR = Van Rensburg. Specimens from BOL, PRE and STE.



FIGURE 8. — *Pentameris longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker. A, habit: erect culms, basally covered in loose, dead leaf sheaths; note long leaf blades, which may be rolled or open, and large, globose, effuse panicle, $\times 0.8$; B, ligule, which is a row of hairs, surrounding leaf parts, with hairs on leaf sheath, expanded auricles, and sparsely pubescent adaxial basal leaf surface, $\times 4.7$.

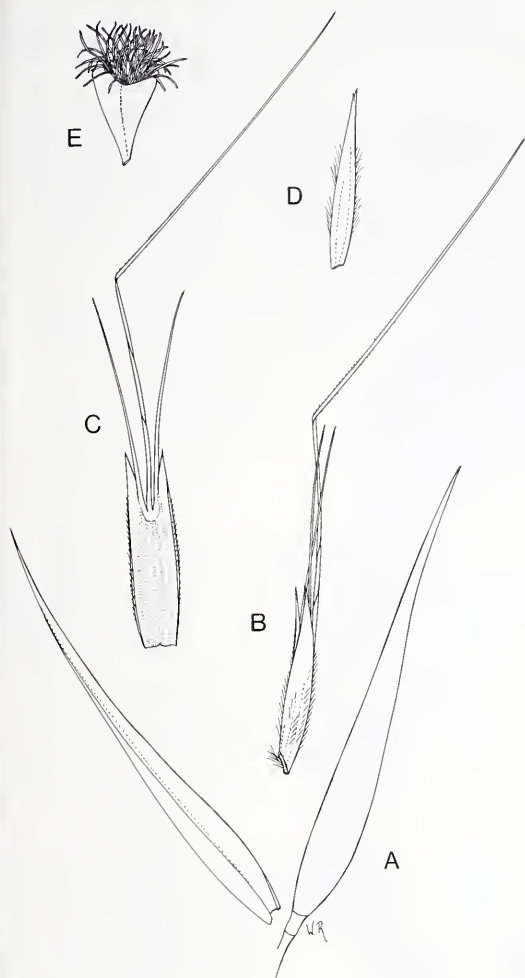


FIGURE 9.—*Pentameris longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker. Parts of spikelet and florets: A, long, acuminate glumes; B, whole basal floret; C, lemma (opened, flattened and viewed from inside of floret) indicating venation, lemma bristles, lemma lobes (adnate to bristles for most of their length) and geniculate awn; D, palea; E, developing fruit, with apical hairs. A–D, $\times 3.7$; E, $\times 11$.

Stapf (1897) describes *P. longiglumis* as only 1.5 to 2 feet (450–600 mm) tall. Nees does not give any indication of plant height, but all specimens of this taxon seen, including the type (*Bergius s.n.*), have far exceeded this height. Furthermore, Stapf describes the sheath as glabrous or sparsely hairy, whereas the type specimen has a distinctly pubescent sheath, as described by Nees (1841). In addition, Stapf describes the leaves as being filiform, 6–9 inches (150–220 mm) long. Nees does not provide leaf lengths in his description, but leaves on the type specimen were noted to be much longer than 6–9 inches, broad, rolled and somewhat rigid.

Furthermore, at least three of the four specimens cited by Stapf under his description of *P. longiglumis* do not match the *Bergius* specimen cited by Nees. The three specimens in question, *Burchell* 542, *Burchell* 598 and *Milne* 246 were obtained from The Herbarium, Royal Botanic Gardens, Kew (K). The fourth voucher cited by

Stapf, *Spielhaus s.n.*, was not traced. Unfortunately these three specimens are of poor quality. The spikelets (when present) are devoid of florets, and one specimen, *Burchell* 542, is entirely sterile. Uncertainty about the identity of the *Milne* 246 specimen is further borne out by an annotation to the effect that the leaves resemble those of *Pentaschistis pallescens* (Schrad.) Stapf, whereas the inflorescence resembles that of *Pentameris thuarii*. The *Burchell* 598 specimen may possibly be *Pentameris longiglumis* as it has floral parts of a size comparable to those observed in Nees's type specimen. However, the basal parts are absent, so the leaf and sheath characters cannot be compared.

It is therefore considered that Stapf's (1897) description and cited vouchers do not agree with Nees's description and type of *P. longiglumis*. Stapf's *Pentameris longiglumis* is therefore regarded as a misapplied name, and it appears that Stapf described a species of *Pentaschistis*.

This subspecies is known from a few specimens collected from Table Mountain, the distribution shown in Figure 5. Until recently, this taxon was thought to be extinct, as the most recent specimen seen among the holdings of eight South African herbaria is dated 1918. However, a small population has been located in a recently burnt area on Table Mountain. This population is growing in a slightly sloping seepage area. The moist habitat requirement matches that of the other subspecies, which is, however, found on steeper slopes.

Vouchers: *N. Barker* 993, 994 (BOL, PRE); *Bews* 15170 (BOL); *Marloth* 3063, 3078 (PRE).

3b. *Pentameris longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker, subsp. nov.

Differt a *P. longiglumi* subsp. *longiglumi* foliorum vaginis glabris et partibus floralibus grandioribus: glumae 21–24 mm longae, lemma 5.0–5.5 mm longum; subspecies tantum monte 'Kogelberg' nominato nota. Figures 2C; 8 & 9.

TYPE.—Cape, summit ridge of Platberg, Kogelberg, S side, edge of gully; culms 3–4 ft. (1.0–1.3 m), erect, coarse, loose tufts, 2650 ft (900 m), 27 Nov. 1967, *Taylor* 7231 (PRE, holo.!, STE, iso.!).

As shown in Table 5, this subspecies differs from *P. longiglumis* subsp. *longiglumis* in a number of features. The subspecific epithet chosen for this species describes one of these distinguishing characters: the glabrous leaf sheaths.

This subspecies is known only from the Kogelberg Forest Reserve (Figure 5). It inhabits south-facing mountain slopes in seepage areas where it forms large tussocks.

Vouchers: *Boucher* 1649 (PRE); *Ellis* 2341 (PRE); *Esterhuysen* 13326 (BOL, PRE); *Stirton & Zantovska* 11293 (STE); *Van Rensburg* 518 (STE).

4. *Pentameris hirtiglumis* N.P. Barker, sp. nov.

P. oreophila similis sed glumis hirsutis facile distincta; lobis lemmae acutis, usque ad dimidium longitudinis ad setam adnatis.



FIGURE 10. — *Pentameris hirtiglumis* N.P. Barker, type specimen *Kerfoot* 6092. A, habit: decumbent, branching culm basally covered in dead leaf sheaths; note that flowering culm is not normally curved back upon itself, but appeared so on specimen. B–G, parts of spikelet and florets: B, hirsute glumes; C, whole basal floret; D, lemma (opened, flattened and viewed from inside of floret) showing venation, lemma bristles, lemma lobes (adnate to bristle for half or less of their length) and geniculate awn; E, palea; F, anthers, with no filaments; G, ovary with apical hairs and stigmas. A, $\times 0.5$; B–F, $\times 4.7$; G, $\times 14$.

TYPE.—Cape, Bosboukloof, Jonkershoek, locally very common, attractive, 980 ft (600 m), Oct. 1967, *Kerfoot 6092* (PRE, holo.).

Plants cushion-like or densely bushy, branched; *culms* somewhat decumbent with numerous nodes, 200–750 mm long; *leaf sheaths* pubescent, at least along margins (rarely glabrous), persistent, not closely appressed to culm, loose when dead; *leaf blades* up to 200 mm long, permanently rolled, falcate; *panicle* lanceolate, somewhat lax, 75–110 × 20–35 mm; *spikelets* 15–50, two-flowered; *glumes* hirsute, 14.5–21.5 × 1.6–2.1 mm; *lemma body* 2.8–3.7 mm long; *lemma lobes* 1–2 mm long, acute, adnate to a 3.0–6.5 mm long lateral bristle for half or less of their length; *awn* geniculate, 4–6 mm from base to knee, 7.5–11.0 mm from knee to tip; *palea* 4.0–4.5 mm long; *lodicules* cuneate, glabrous; *anthers* 3.5–5.0 mm long; *fruit* broadly fusiform, 2.4 × 1.2 mm, surface colliculately sculptured (Figure 1A); *flowering time* September to October/November.

This species is similar in appearance to *P. oreophila*, but can be readily separated from that species by the presence of the hirsute glumes (Figure 10B). Additional differences between these two taxa are the acute lemma lobes (Figure 10D) and softer, non-pungent leaf apices in *P. hirtiglumis*. However, as is apparent from the cladogram discussed above (Figure 3), this species is sister to *P. longiglumis* on the basis of several anatomical features including swollen leaf margins, inflated abaxial epidermal cells and dense, strongly inclined adaxial prickles.

Like *P. oreophila*, this taxon has a geographically restricted distribution, and is known only from high montane regions of the Hottentots Holland Mts (Figure 5). Where found, this species is abundant and locally dominant. However, it appears to have narrow habitat requirements, and is restricted to shale bands.

Vouchers: *N. Barker 90* (PRE); *Ellis 4680* (PRE); *Kruger & Haynes 753* (JF, STE).

5. *Pentameris macrocalycina* (Steud.) Schweick. in Feddes Repertorium 43: 91 (1938); N.P. Barker in Gibbs Russell *et al.*: 252. (1990). Type: Cape, in summitate Montis Tabularis Ecklon 932 (OXF, lecto., PRE islecto.!, (fragments), S, islecto.!). Lectotype here designated.

Avena macrocalycina Steud.: 482 (1829).

Danthonia speciosa Lehm. ex Nees: 307 (1841). Steud.: 241. (1855); Durand & Schinz: 854 (1895). Type: In apicis rupestris montis ad Genadenhal solo sabuloso-humoso alt. 2000–3000 ft. (Stellenbosch), et in Dutoitskloof alt. 2500–3000 ft. *Drège s.n.* (PRE fragments, iso!).

Pentameris speciosa (Lehm. ex Nees) Stapf: 515 (1897).

Plants caespitose, branched; *culms* 0.43–1.10 m long; *leaf sheaths* sometimes bearded at mouth, persistent, closely appressed to culm; *leaf blades* 110–290 mm long, acicular; *panicle* lanceolate, somewhat lax, 60–120 × 10–60 mm; *spikelets* 10–50, two-flowered; *glumes* 16–24 × 2–3 mm; *lemma body* 3.5–5.5 mm long; *lemma lobes* 1.3–4.0 mm long, acute-acuminate, adnate to a 7.5–12.0 mm long lateral bristle for most of their length; *awn* geniculate, 5.5–10.0 mm from base to knee, 9–16 mm from knee to tip; *palea* 6.5–11.0 mm long; *lodicules* cuneate,

glabrous; *anthers* 4.2–6.0 mm long; *fruit* broadly fusiform, 3.6 × 1.2 mm, surface colliculately sculptured; *flowering time* September to December.

Schweickerdt (1938) pointed out that both Stapf (1897) and Durand & Schinz (1895) had placed *Avena macrocalycina* in synonymy under *Danthonia macrantha*. In addition, Nees (1832) mistakenly placed *Avena macrocalycina* and its type, Ecklon 932, under *Pentameris macrantha*. This confusion arose as a result of the fact that there were two specimens representing different taxa distributed under the number Ecklon 932. The type specimen of *Avena macrocalycina*, one of the Ecklon 932 specimens, was obtained from the Fielding-Druce herbarium, Oxford (OXF), and is designated here as the lectotype. A duplicate of this specimen is housed in the Swedish Museum (S).

This is a widely distributed species, recorded from Pakhuis Pass in the north to Cape Point in the south and eastwards to the Groendal Wilderness Reserve (Figure 11).

Vouchers: *Adamson 3980* (JF, PRE); *Ellis 2540* (PRE); *Esterhuysen 23763, 28012* (BOL, PRE); *Taylor 11113* (PRE, STE).

6. *Pentameris oreophila* N.P. Barker, sp. nov.

Species laminis revolutis permanentibus, brevibus (<105 mm longis), falcatis, et foliorum vaginis saltem marginibus pubescentibus distinguatur.

Pentameris sp. 1. in Gibbs Russell *et al.*: 252. (1990).

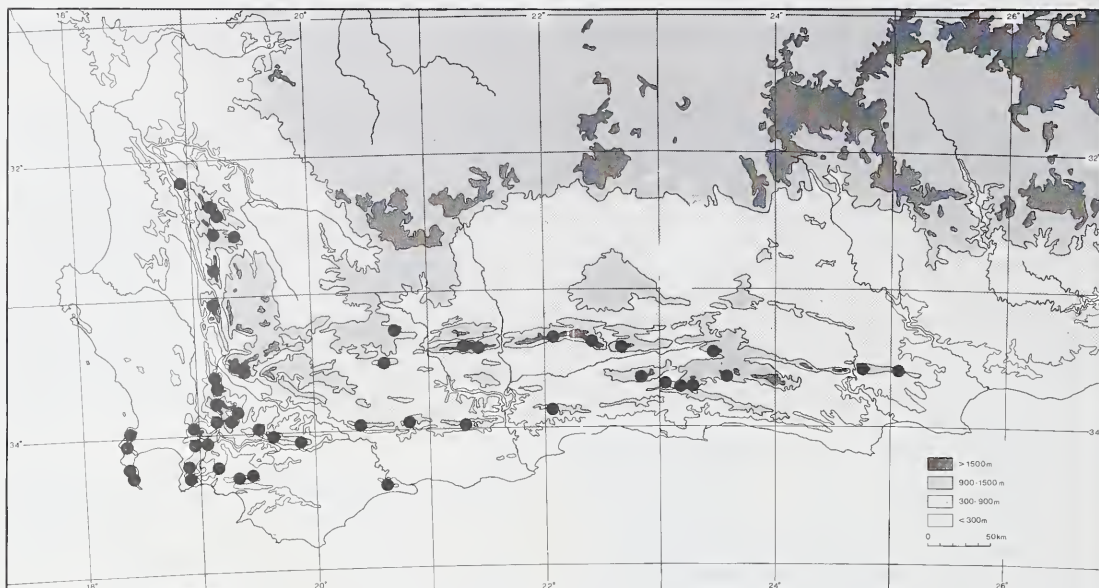
P. obtusifolia sensu Ellis (1985d), Barker (1986, 1989). Note that *P. obtusifolia* (Hochst.) Schweick. is to be transferred to *Pseudopentameris*.

TYPE.—Cape, Worcester Div., Jona's Kop, common on shale band, or on peaty slopes, after fire, in different aspects but not on steep southern slopes, forming dense and, in some places, quite extensive patches, leaf tips very sharp, 5000 ft (1 500 m), 19 Dec. 1971, *Esterhuysen 32681* (PRE, holo.!, BOL, iso!).

Plants cushion-like or densely bushy, branched basally; *culms* erect or somewhat decumbent in older, larger tufts and then with numerous nodes, up to 530 mm long; *leaf sheaths* persistent, pubescent along margins, appressed or free from culm, especially when dead, often purple when young; *leaf blades* up to 105 mm long, permanently rolled, falcate (less so in young plants), strongly pungent; *panicle* lanceolate, somewhat lax, 30–80 × 20–40 mm; *spikelets* 8–20, two-flowered; *glumes* 14–20 × 2.1–3.0 mm; *lemma body* 3–4 mm long; *lemma lobes* 1.6–3.0 (–4.0) mm long, acuminate, adnate to 7.0–10.5 mm long lateral bristle for most of their length; *awn* geniculate, 6–11 mm from base to knee, 9.5–13.0 mm from knee to tip; *palea* 5.5–8.5 mm long; *lodicules* cuneate, glabrous; *anthers* 4.0–5.5 mm long; *fruit* subglobose, 3.5–4.0 × 1.6–2.0 mm, surface colliculately sculptured; *flowering time* September to December. Figures 1E & 2B.

The species can be distinguished by its permanently rolled, short (<105 mm long), falcate leaf blades and the leaf sheaths which are pubescent at least along the margins.

The specific epithet *oreophila*, or 'mountain-loving', is chosen because this species is only found at high altitudes in the Hottentots Holland, Riviersondereinde and Hex

FIGURE 11.—Distribution of *P. macrocalycina*.

River Mountain ranges (Figure 5). Where found, the species is abundant, especially in years immediately after fire. Its high altitude habitat receives snow in the winter months, and the cushion-like growth form (Figure 12) may be an adaptation to this.

Vouchers: Ellis 4686 (PRE); Esterhuysen 19788 (BOL, PRE); Forsyth 191 (JF, PRE); Phillips 2109 (SAM); Wasserfall 562 (BOL, NE.G).

7. *Pentameris distichophylla* (Lehm.) Nees in Linnaea 7: 314. (1832); Kunth: 317 (1833). Type: Habitat in Promontorio Bonae Spei, collector unknown (S, lecto!., PRE, fragment).

Danthonia distichophylla Lehm.: 41 (1831); Nees: 305 (1841).

Pentameris dregeana Stapf: 515 (1897); N.P. Barker in Gibbs Russell et al.: 252 (1990).

Plants caespitose, becoming cushion-like with age, branched basally; *culms* 0.4–1.2 m long; *leaf sheaths* pubescent to woolly, especially near mouth, appressed to culm, persistent; *leaf blades* 80–190(–300) mm long, pubescent, rolled, folded or flat; *panicle* lanceolate, somewhat lax, 50–110 × 15–60 mm; *spikelets* 12–65, two-flowered; *glumes* 12–15 × 1–2 mm, occasionally sparsely pubescent; *lemma body* 2.3–3.5 mm long; *lemma lobes* 1.0–2.6 mm long, acute, adnate to a 5.0–10.5 mm long lateral bristle for most of their length; *awn* geniculate, 4–7 mm from base to knee, 6–12 mm from knee to tip; *palea* 4–6 mm long; *lodicules* cuneate, glabrous or shortly ciliolate, rarely with arm-like extensions; *anthers* 3.0–4.5 mm long; *fruit* cuneate, 2.0 × 0.9 mm, surface rugosely sculptured; *flowering time* September to December. Figures 1 & 2.

Stapf (1897) created the epithet *dregeana* for the partial concept of the taxon which Nees (1841) called *Danthonia distichophylla*. Stapf did not agree with Nees on the

inclusion of Lehmann's description of *Danthonia distichophylla*, and in a footnote states that Lehmann's description probably refers to a *Pentaschistis*. It thus appears that Stapf did not see the type of Lehmann's *Danthonia distichophylla*.

Lehmann's description (1831) states that he has seen the specimen in a dried state (v.s. = *vide siccam*). According to Nordenstam (1980), Lehmann's herbarium comprised many specimens collected by Ecklon & Zeyher. The collections of Lehmann now reside in the Swedish Museum of Natural History (S), from which the type of *Danthonia distichophylla* was obtained. The label of this specimen had been annotated (possibly by Nordenstam) to the effect that it is written in Lehmann's hand. Further confirmation of this was obtained by matching the script with that of published examples of Lehmann's handwriting (Burdet 1976; Nordenstam 1980). As there are no other labels on the specimen, the original collector of this specimen is unknown, but as Lehmann never visited southern Africa, it is possible that the specimen is an Ecklon & Zeyher collection.

Despite Stapf's comment, the Lehmann specimen is a good match to the specimens of *P. dregeana* cited by Stapf (1897). The name *P. dregeana* is therefore illegitimate as it is antedated by Lehmann's *P. distichophylla*. This taxon is therefore correctly named *Pentameris distichophylla* (Lehm.) Nees. As there is no conclusive evidence that the Lehmann specimen from S is the holotype, it is designated as the lectotype.

This species is one of the most widely distributed in the genus, ranging from the northern Cedarberg to Paarl and eastwards to the Tsitsikamma Mountains (Figure 13).

Vouchers: Esterhuysen 22352, 27321 (BOL, PRE); Hafstrom & Acocks 45 (PRE); Gillett 3835 (STE); Taylor 11590 (PRE, STE).

8. *Pentameris swartbergensis* N.P. Barker, sp. nov., *P. distichophyllae* similis sed foliorum vaginis glabris differt.

TYPE.—Cape, Toverkop, Swartberg nr Ladismith, broad ledges at base of high cliffs on S side of peak, appears to be locally dominant below cave, 6500 ft. (1 875 m), 17 Dec. 1956, *Esterhuysen* 26755 (PRE, holo.!, BOL, iso.!).

Plants caespitose or somewhat decumbent, basally branched; *culms* up to 560 mm long; *leaf sheaths* glabrous, appressed to culm; *leaf blades* up to 230 mm long, folded or rolled, sparsely pubescent near base; *panicle* lanceolate, 80–90 × 20–35 mm, somewhat lax; *spikelets* 22–56, two-flowered; *glumes* 11.5–13.0 × 1.5–1.6 mm; *lemma body* 2.8–3.0 mm long; *lemma lobes*, acuminate,

1.4–1.5 mm long, adnate to 2.5–3.5 mm long lateral bristle for about half their length; *awn* geniculate, 3 mm from base to knee, 5.5–7.0 mm from knee to tip; *palea* 4.5–5.0 mm long; *lodicules* cuneate, ciliolate at apex; *fruit* broadly fusiform, 2.0–2.4 × 1.0 mm, surface colliculately sculptured; *flowering time* September to December. Figure 14.

This species may be confused with *P. distichophylla*, but differs in such features as the nature of the colliculate surface of the caryopsis (which is rugose in *P. distichophylla*), the leaf sheaths (glabrous in *P. swartbergensis*, pubescent to woolly in *P. distichophylla*) and the lateral lemma bristles, which are substantially shorter in *P. swartbergensis*.

This taxon is known from only two localities in the Klein Swartberg, and is probably endemic to this mountain range

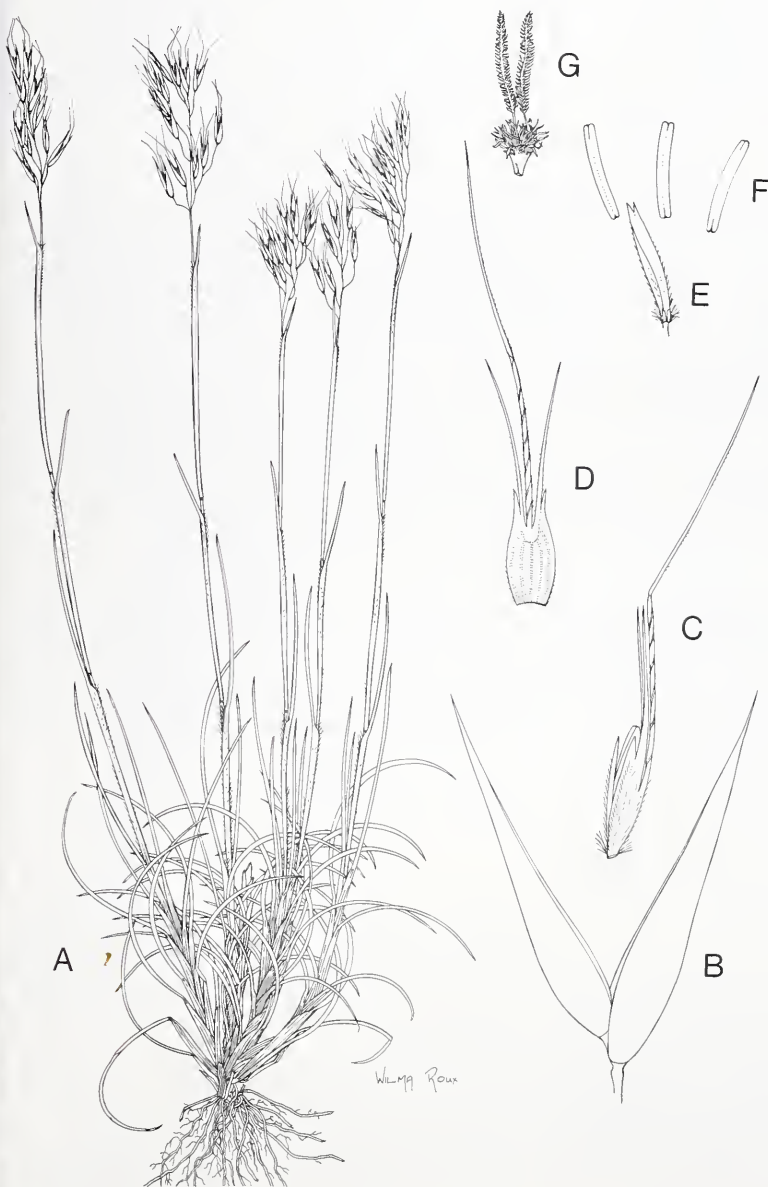


FIGURE 12.—*Pentameris oreophila* N.P. Barker. A, habit: erect culms and prickly, cushion-like basal leaf growth; note also pubescent leaf sheaths loosely appressed to stems, falcate, permanently rolled leaf blades with pungent apices. B–G, parts of spikelet and florets: B, glumes; C, whole basal floret; D, lemma (opened, flattened and viewed from inside of floret) showing venation, lemma bristles, lemma lobes (adnate to bristles for most of their length) and geniculate awn; E, palea; F, anthers with no filaments; G, ovary with apical hairs and stigmas. A, × 0.3; B–F, × 3.7; G, × 11.

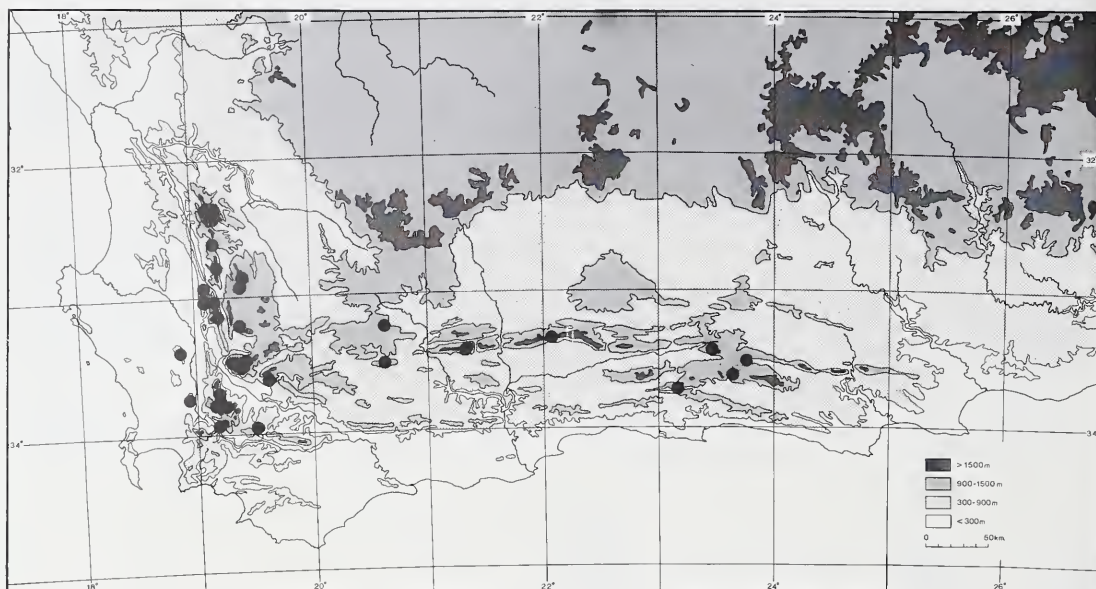


FIGURE 13.—Distribution of *P. distichophylla* (Lehm.) Nees.

(Figure 5). It grows at the foot of cliffs or rock walls in deep shade.

Vouchers: Esterhuysen 18510, 26750, 26751 (BOL, PRE); Linder 5490 (BOL).

9. *Pentameris glacialis* N.P. Barker, sp. nov., a *P. distichophylla* spiculis paucis (<15), foliis brevibus filiformibus et habitu decumbenti molli distinguitur.

TYPE.—Cape, Oudtshoorn, Waboomsberg, growing in humic gullies on south slopes, 14 Dec. 1991, N.P. Barker 995 (BOL, holo.!; B, CANB, G, GRA, J, K, NBG, NSW, NU, P, PRE, STE, all iso.)

Plants decumbent; *culms* thin, flexuous, up to 550 mm long, tinged with purple; *leaf sheaths* glabrous or pubescent along margins, loosely appressed to culm; *leaf blades* filiform, short, up to 100 mm long, rolled; *panicle* lanceolate, to 70 × 30 mm, lax to somewhat contracted; *spikelets* 6–12(–15), two-flowered; *glumes* 13.0–14.5 × 1.3–1.5 mm; *lemma body* 2.5–3.0 mm long; *lemma lobes* acuminate, 1.0–1.9 mm long, adnate to 3.5–4.5 mm long lateral bristle for less than half its length; *awn* geniculate, 3.5–5.5 mm from base to knee, 7.5–8.5 mm from knee to tip; *palea* 3.5–4.2 mm long; *lodicules* cuneate, glabrous; *fruit* an achene, 2.5 × 1 mm, surface colliculately sculptured; *flowering time* October to December.

This species, first collected in 1987 by Ellis, bears superficial resemblance to *P. macrocalycina*, but is distinguishable from that species by the slender, geniculate culms, the rolled but not acicular leaf blades, the panicles with few spikelets, as well as by the size of the floral structures, which are substantially smaller in *P. glacialis*. The species is generally found to be locally abundant, growing in narrow gullies, rock ledges and overhangs in black, humic but sandy soils. Such habitats are thought

to become particularly heavily snowed up in winter. This habitat appears to preclude *P. macrocalycina*, which is found in more stony sites, as well as *P. distichophylla*, which appears to prefer northern aspects and rock crevices. The woolly leaf bases and sheaths of *P. distichophylla* separate this species from *P. glacialis* (Figure 15).

When visited in mid-October 1991, the plants and rocks at the type locality were covered in a thick layer of ice. Such conditions may persist for three or more months of the year in the winter and spring, depending on the severity of the frontal systems associated with the winter rainfall regime of the southwestern Cape. This harsh, icy environment gave rise to the specific epithet.

A subsequent visit in mid-December 1991 provided an indication of the range of climatic extremes in which this species survives, with very hot, dry conditions prevailing. The steep-sided, rocky gullies in which this species is found were, however, cooler, being shaded for much of the day, and the humic soil was still damp. Figure 5 shows the distribution of this species.

Vouchers: N. Barker 995, 996 (BOL, GRA, J, NBG, S, STE, UWC), 997 (BOL, K, PERTH, PRE), 1019 (BOL); Ellis 5620 (PRE).

INCERTAE SEDIS

A single unusual specimen, undoubtedly belonging to the genus *Pentameris* (possessing an achene with apical hairs) was collected from Cockscomb Peak by Ellis in 1987. This specimen, Ellis 5605 (PRE), is morphologically similar in certain respects to *P. glacialis*, but differs in its leaf anatomy.

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FIGURE 14. —*Pentameris swartbergensis* N.P. Barker. A, habit: erect culms (folded back, based on type material) and branched basal parts. B–F, parts of spikelet and florets: B, glumes; C, whole basal floret; D, lemma (opened, flattened and viewed from inside of floret) showing venation, lemma bristles, lemma lobes (adnate to bristles for most of their length) and geniculate awn; E, palea; F, developing fruit with apical hairs, note that fruit appears to develop in a basipetal direction, uppermost region becoming swollen and associated surface sculptured, appearing at apex first. A, $\times 0.5$; B–E, $\times 4.8$; F, $\times 14.6$.



FIGURE 15.—*Pentameris glacialis* N.P. Barker. A, habit: showing thin, decumbent culms; B, indumentum of sheath, pubescent along margin, sheath mouth and leaf blade. C–H, parts of spikelet and florets: C, glumes; D, whole basal floret with mature fruit; E, lemma (opened, flattened and viewed from inside of floret) showing venation, lemma bristles, lemma lobes (adnate to bristles for about half their length) and geniculate awn; F, palea; G, fruit with apical hairs; H, spikelet. A, $\times 0.4$; B–F, $\times 3.7$; G, $\times 6$; H, $\times 2.4$.

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Studies in the Marchantiales (Hepaticae) from southern Africa. 1. The genus *Dumortiera* and *D. hirsuta*; the genus *Lunularia* and *L. cruciata*

S.M. PEROLD*

Keywords: *Dumortiera*, *D. hirsuta*, Dumortieroideae, Hepaticae, *Lunularia*, *L. cruciata*, Lunulariaceae, Marchantiaceae, Marchantiales, taxonomy, southern Africa, Wiesnerellaceae

ABSTRACT

The genera *Dumortiera* (Dumortieroideae, Marchantiaceae) and *Lunularia* (Lunulariaceae), are briefly discussed. Each genus is represented in southern Africa by only one subcosmopolitan species, *D. hirsuta* (Swartz) Nees and *L. cruciata* (L.) Dum. ex Lindberg respectively.

UITTREKSEL

Die genusse *Dumortiera* (Dumortieroideae, Marchantiaceae) en *Lunularia* (Lunulariaceae) word kortliks bespreek. In suidelike Afrika word elke genus verteenwoordig deur slegs een halfkosmopolitiese spesie, *D. hirsuta* (Swartz) Nees en *L. cruciata* (L.) Dum. ex Lindberg onderskeidelik.

DUMORTIERA Nees

Dumortiera Nees ab *Esenbeck* in Reinwardt, Blume & Nees ab *Esenbeck*, Hepaticae Javanicae, Nova Acta Academiae Caesareae Leopoldina-Carolinae Germanicae Naturae Curiosorum XII: 410 (1824); Gottsche *et al.*: 542 (1846); Schiffner: 35 (1893); Stephani: 222 (1899); Sim: 25 (1926); Müller: 394 (1951–1958); S. Arnell: 52 (1963); Hässel de Menéndez: 182 (1963). Type species: *Dumortiera hirsuta* (Swartz) Nees.

Synonymy according to Nelson & Parnell: 35 (1992):

Hygophylla Taylor: 390 (1836).

Hygrophila Taylor (orth. var.) in Mackay: 53 (1836) non R. Br. (1810).

Hygophylla Taylor (orth. var.) in Mackay: X (1836).

Hygrophila Taylor (orth. var.) in J.D. Hooker & T. Taylor: 576 (1844).

Askepos Griffith 2: 340 (1849).

Thallus, large, flat and thin, dark green, in overlying patches; on shaded, damp soil or on wet rocks. Branches with apical innovations or dichotomously furcate, occasionally lateral, moderately divergent, thickened over midrib, wings gradually thinning toward margins; apex emarginate.

Dorsal epidermis very thin-walled, temporary, vestigial, air pores absent, air chambers mostly reduced to 1- or 2-celled vestiges, reported rarely to have reduced chlorophyllose filaments, cells containing numerous fairly large chloroplasts; storage tissue compact, confined to ventral part of midrib; oil cells rare, each with a single, large oil body; rhizoids along midrib and ventrally appressed against wings, mostly smooth, occasionally tuberculate; scales ventral over midrib, vestigial and evanescent.

Monoicous or dioicous. *Antheridia* sunken in subsessile disciform receptacles, which are fringed with bristles and borne singly at apex of thallus on short bifurrowed stalk. *Archegonia* in groups of 8–16 in saccate, fleshy involucre, on lower surface of 6–8-lobed disciform receptacle with marginal sinuses dorsally, raised on stalk with two rhizoidal furrows; after fertilization and maturation, each involucre generally containing a single sporophyte consisting of foot, seta and capsule; capsule wall unistratose, with annular thickenings, dehiscing irregularly. *Spores* small, papillose. *Elaters* slender, tapering, 1–3-spirate. *Gemmae* absent.

Dumortiera hirsuta (Swartz) Nees in Reinwardt, Blume & Nees ab *Esenbeck*, Nova Acta Academiae Caesareae Leopoldina-Carolinae Germanicae Naturae Curiosorum XII: 410 (1824); Gottsche *et al.*: 542 (1846); Spruce: 566 (1885); Stephani: 224 (1899); Macvicar: 41 (1926); Sim: 25 (1926); Müller: 396 (1951); S. Arnell: 52 (1963); Hässel de Menéndez: 182 (1963). Type: Jamaica, leg. Swartz s.n. [S, holo.!: MW, iso. (Hb. Hoffm. No. 8497); UPS, fide Grolle 1976].

Marchantia hirsuta Swartz: 145 (1788).

M. irrigua Wilson ex Hooker in Smith: 106 (1833). *Hygophylla irrigua* (Wilson) Taylor: 390 (1836); Mackay: 54 (1836); Stephani: 150 (1899). *Dumortiera irrigua* (Wilson) Nees: 159 (1838). *D. hirsuta* var. *irrigua* (Taylor) Spruce: 566 (1885). Type: Ireland, Turk Cascade, near Killarney, Mr Wilson.

D. hirsuta var. *angustior* Gottsche, Lindenberg & Nees: 544 (1846).

D. hirsuta var. *intermedia* Gottsche, Lindenberg & Nees: 544 (1846).

D. velutina Schiffner: 256 (1893).

Askepos brevipes Griffith: 340 (1849). Type: India, in sylvis umbrosis Tingrei agri, II 1836.

Thallus hygrophylous, large and creeping, broadly and rather irregularly strap-shaped, uniformly dark green, translucent, thin and flat, but often marginally undulate, wet (Figure 1A); crisped and shrivelled, dull, unable to survive dry; in crowded, overlying patches, once to several times dichotomously or occasionally laterally furcate or

* National Botanical Institute, Private Bag X101, Pretoria 0001.
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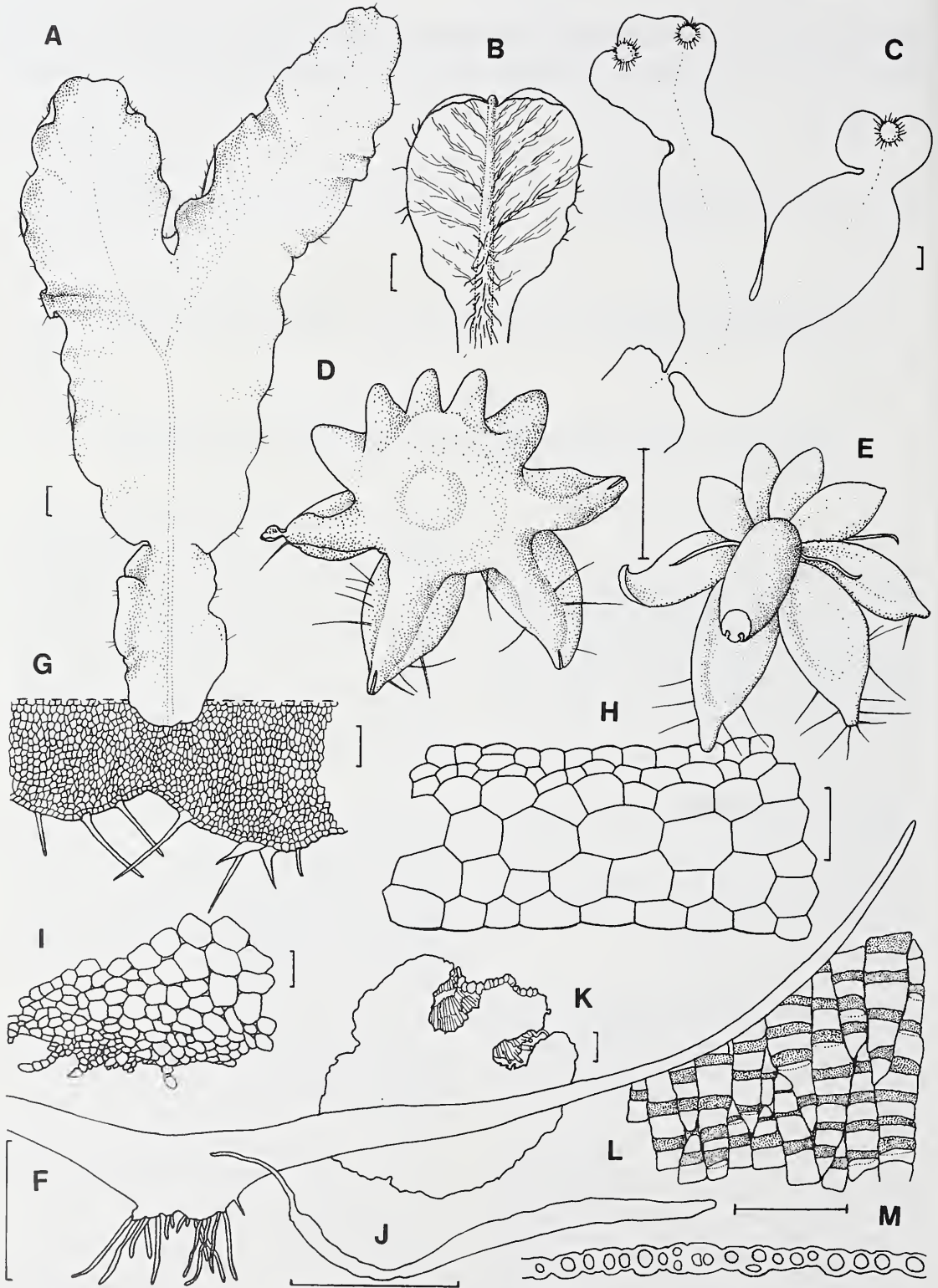


FIGURE 1. —*Dumortiera hirsuta*. A, dorsal view of thallus; B, ventral view of thallus; C, male plant with disciform receptacles at apex; D, young female receptacle seen from above; E, young female receptacle seen from below; F, transverse section of thallus; G, margin of thallus with hairs; H, transverse section of thallus, much enlarged; I, lower cells of costa and vestigial scales in transverse section; J, filiform scale from top of stalk; K, transverse section of stalk with two rhizoidal furrows; L, capsule wall cells with thickenings; M, transverse section of capsule wall. A, F–H, *S. M. Perold* 2694; B, *S. M. Perold* 2634; C, *Nicholas* 1176; D, E, I, *H. Anderson* CH 13495; J–L, *Doidge* CH 3581. Scale bars: A–C = 2 mm; D–F, J = 1 mm; G, K = 100 μ m; H, I, L, M = 50 μ m. Illustrations by G. Condy.

with apical innovations; branches $50-95 \times 8-13(-22)$ mm and ± 500 μ m thick over median, ventrally bulging midrib (also visible from above), laterally gradually thinning out into wide wings (Figure 1F); apex shortly emarginate; margins undulate, occasionally scalloped, sparsely hirsute, hairs ± 250.0 μ m long, ± 12.5 μ m wide at base, tapering slightly to somewhat blunt tip (Figure 1G).

Epidermis, pores and air chambers absent; dorsal cells from above, 4–6-sided, variable in shape and size, $27-57 \times (17-)$ $22-32$ μ m, in cross section ± 15 μ m thick, containing chloroplasts; marginal cells thin-walled, long- or short-rectangular, $25-62 \times 12-20$ μ m; midrib with ± 18 rows of cells of which upper 3 rows larger, rounded, up to 100×137 μ m, with somewhat wavy walls and scattered chloroplasts, lower group of cells angular, smaller, ± 30 μ m wide, lacking chloroplasts; wings medianly with 3 rows of large cells, decreasing in number to one row at margin, covered by dorsal and ventral layer of smaller chlorophyllose cells; oil bodies quite rare, for the most part confined to scattered cells in the midrib, yellow-brown, elongate or round, ± 40 μ m across; rhizoids below midrib numerous, mostly smooth, $15-20$ μ m wide, occasionally tuberculate, 5 μ m wide, also in widely spaced, arching strands below wings, radiating toward margins and appressed to ventral face of wings (Figure 1B) or scattered; ventral scales hyaline, vestigial (Figure 1I), without appendages, evanescent, only near apex.

Monoicous or dioicous. *Antheridiophore* subsessile, disciform, 2.75 mm in diameter, 0.6 mm thick in centre, flattening toward sides, containing antheridia, 470×250 μ m, \pm ovate, acropetally arranged, but not in radiating rows, sunken into disc, borne singly at apical notch of thallus (Figures 1C; 2A) on very short, 1 mm diameter, bifurrowed stalk, with rhizoids lining furrows; hyaline, filiform scales on ventral face of disc, the latter encircled by dense outer fringe of bristle-like hairs, $600-1100$ μ m long, base $20-25$ μ m wide, a few scattered hairs dorsally. *Archegoniophore* disciform, 3.75 mm in diameter; dorsal face (Figure 1D) becoming radially grooved by sinuses; ventral face 6–8-lobed (Figure 1E) in radiating rows and then almost star-shaped, sparingly bristled; archegonia in groups of 8–16, enclosed in green, fleshy, saccate involucre, long archegonial necks protruding through narrow slit-like apical openings; receptacle eventually raised on stalk arising at apical notch of thallus between overlapping sides, ± 40 mm long and ± 925 μ m wide, cortical cells $\pm 15.0 \times 12.5$ μ m, inner cells $\pm 50 \times 30$ μ m; along its length 2 furrows lined with rhizoids (Figure 1K) and its top (where joined to disc) encircled by numerous filiform, hyaline scales (Figure 1J), up to 3750 μ m long and 300 μ m wide at base, apex only ± 3 cells wide, cells mostly $\pm 125 \times 22$ μ m; at maturity generally only one sporangium borne in each involucre, rarely two and quite often none, elliptical, 2.5×1.5 mm, supported on elongating seta and protruding from membranous calyptra, pseudoperianth lacking; capsule wall unistratose (Figure 1M) with annular or semi-annular thickenings (Figure 1L), dehiscing irregularly via longitudinal suture lines and releasing large numbers of elaters and spores (Figure 2B). *Spores* golden brown, semi-transparent, distal face rounded, proximal face \pm flat to slightly peaked in the centre, triradiate mark indistinct, $25-30$ μ m across its longer axis, ornamented with numerous nodules or

tubercles, irregular in size and shape (Figure 3A). *Elaters* yellow-brown or orange-brown, mostly with doubly spiral strands (Figure 3B), ends tapering, $225-470 \times 7.5-10.0$ μ m in middle and 3.5 μ m wide at tips. *Gemmae* absent.

Chromosome number: $n = 9$ (Berrie 1960, Bornefeld 1987); $n = 18$ (Tatuno 1941); $n = 27$ (Tatuno 1941, Berrie 1958). According to Tatuno (1938, 1939) the 9, 18 and 27 chromosome sets present different races with different distributions and edaphic ecology, but he considers them as belonging to the same species.

Only a few of the specimens examined were fertile; most of these were dioicous, with male and female receptacles borne on separate plants. Monoicous plants were quite rarely found, but have frequently been reported in the literature and even bisexual receptacles are known (Evans 1919).

All southern African specimens have been identified as belonging to *D. hirsuta*: the dorsal face of the thallus is always \pm smooth and lacks papilliform cells or traces of air chambers. *D. nepalensis* and *D. velutina*, which our material resembles, are considered to belong to the polymorphic species *D. hirsuta* (Grolle & Piippo 1984). Arnell (1963) referred to material from southern Africa (Cape Province, Transvaal, Natal) as *D. hirsuta* var. *nepalensis*. Schuster (1992) considers *D. nepalensis* (Taylor) Nees to be a distinct taxon under the name of *D. hirsuta* subsp. *nepalensis* (Taylor) Schuster which is not found in Africa. *D. hirsuta* is subcosmopolitan and is widespread in tropical and temperate regions, generally growing in sheltered, wooded, shaded and damp areas, i.e. it is hygrophilous. In southern Africa it is known from northern and eastern Transvaal, Swaziland, Natal, Zululand and eastern, southern and southwestern Cape (Figure 4). Further northwards in Africa, *D. hirsuta* is reported from (or has been collected in) Zimbabwe (Best 1990), Zambia [S.M. Perold 2670 (PRE)], East African Mountains (Arnell 1956), East Africa (Bizot *et al.* 1985), Tanzania, Malawi, Mozambique (Bizot & Pócs 1979), Rwanda and Burundi (Vána *et al.* 1979).

On the basis of flavonoid data, Campbell *et al.* (1979) found chemical affinities between *Dumortiera* and *Wiesnerella*, suggesting that they belong in a common family, Wiesnerellaceae (Inoue 1976). This was accepted by Grolle (1983), but Schuster (1984) has retained *Dumortiera* in the Marchantiaceae, creating a new subfamily, Dumortieroideae Schust., for it and designating *Dumortiera* as the type genus. *Dumortiera* has also been classified in the Dumortieroideae by Bischler (1988), who regards *Dumortiera* and *Wiesnerella* as morphologically remotely related, although having similar flavonoid patterns. The treatment of Schuster (1984) is followed here, even though the phylogenetic position of *Dumortiera* remains a matter of some controversy, as conceded by Schuster (1984). Supporting the above treatment are terpene studies of the genera by Asakawa *et al.* (1979, 1980a, 1980b, 1981), who found that *Wiesnerella denudata* and *Conocephalum conicum* shared 17 of these terpene compounds, but only had three in common with *Dumortiera hirsuta*. Luteolin 5-O-glucuronide, the flavonoid shared by *Dumortiera* and *Wiesnerella* which was considered diagnostic for the Wiesnerellaceae by Campbell *et al.* (1979), has since also been

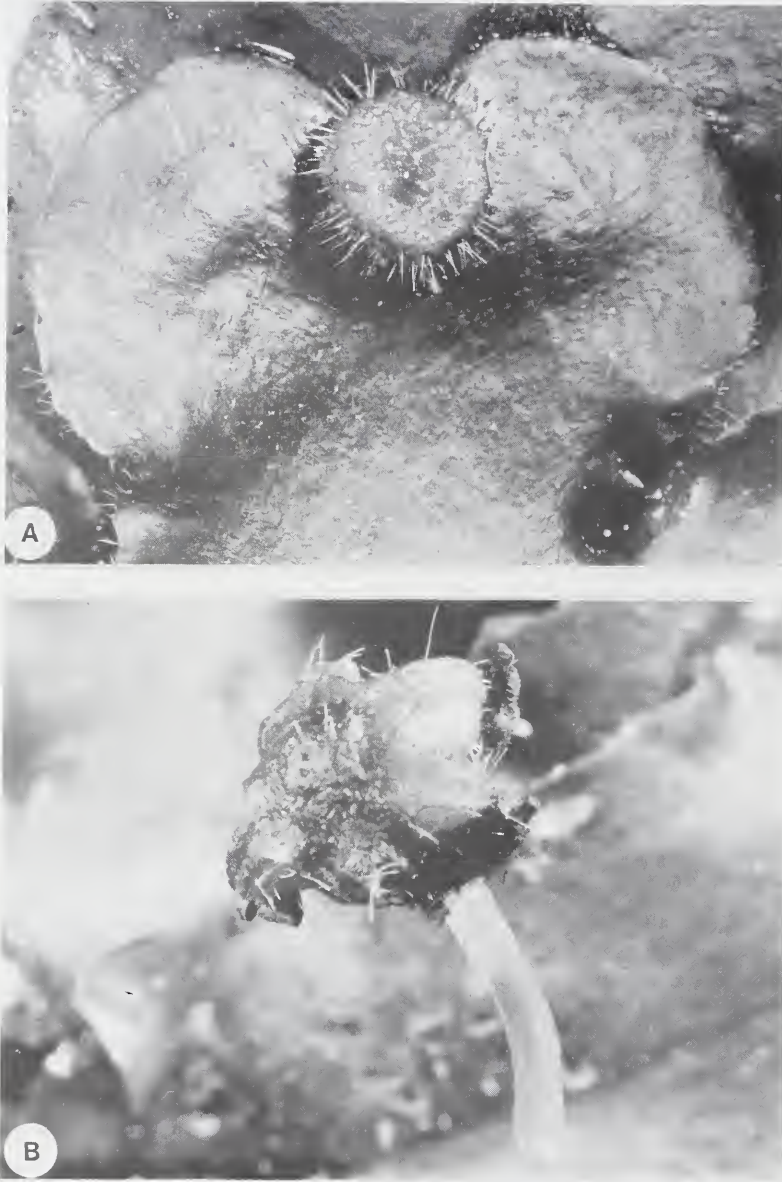


FIGURE 2. —*Dumortiera hirsuta*. A, male plant with sub sessile antheridiophore from above; B, stalked archegoniophore with dehiscent sporangia, front one releasing many spores and elaters. A, B, Koekemoer 989, $\times 9$.

reported for *Conocephalum* by Porter (1981). Whittemore (1991) therefore cautions against drawing taxonomic conclusions from a small number of compounds.

SPECIMENS EXAMINED

TRANSVAAL. —2230 (Messina): Entabene, (—CC), *Bottomley* (PRE); Entabene, (—CC), *Schelpa* 6020 (BOL); Soutpansberg, Entabene, (—CC), *Thomas* 856 (PRE). 2329 (Pietersburg): Pietersburg, (—CD), *Van Vuuren* 1469 (PRE); Haenertsburg, (—DD), *Puterill* 3604 (PRE). 2330 (Tzaneen): Woodbush For. Res., Magoebaskloof, near stream, (—CC), *H. Anderson* CH 13495, CH 13499 (PRE); *Bosman* 3188, (PRE); De Hoek For. Res., Debengeni Falls, on stream bank, beyond foot bridge, (—CC), *S.M. Perold* 2634 (PRE); Woodbush, locally abundant in deep shade on streambank, (—CC), *Schelpa* 6070 (BOL). 2331 (Phalaborwa): Letaba, (—DC), *Scheepers* 984 (PRE). 2430 (Pilgrim's Rest): Farm Cyprus near Ofcolaco, in gorge named 'Terrible Hollow', (—AB), *H. Anderson* CH 4527 (PRE); Mariepskop Forestry Water Works, on outside of water-tank, also under overhang, dense shade, (—DB), *Vorster* 87C (PRE); Mariepskop, near dam in Klaserie River, montane forest, on rock against bank next to stream, in shade, (—DB), *Vorster* 572; Mariepskop For.,

Bedford footpath in forest on soil of streambed, full shade, (—DB), *Vorster* 1398 (PRE); Mariepskop For., Blyde River footpath, on exposed tree root at streamside in forest shade, (—DB), *Vorster* 1472 (PRE); Mariepskop, Blyde River footpath, hanging from vertical sandstone rocks in forest shade, (—DB), *Vorster* 1473 (PRE); Mariepskop, Magalieskop Res. For., on damp earth bank, dense shade, (—DB), *Vorster* 1815 (PRE); Mariepskop, (—DB), *Van der Schijff* 4482 (PRE); Mariepskop, Klaserie River by dam, beneath rocks, (—DB), *Van der Schijff* 6291 (PRE); Mount Sheba Nat. Res., at the 'Grotto', on dripping cliffs, forming extended mats on wet vertical rock face, (—DC), *Jacobsen* 4421 (PRE); Mount Sheba Nature Reserve at the 'Grotto', on dripping rock cliffs, (—DC), *Perold & Koekemoer* 2864 (PRE); Pilgrim's Rest, (—DD), *Van der Schijff* 6367 (PRE). 2527 (Rustenburg): Nature Res. Cederbergkloof, near Utopia, (—CA), *Koekemoer* 972 (PRE). 2530 (Lydenburg): Farm Klipsteen, between Lydenburg and Dullstroom, at waterfall, on rock, (—AB), *H. Anderson* CH 13446 p.p. (PRE); Sabie, Lone Creek Falls, on soil near footpath, (—BA), *S.M. Perold* 2694 (PRE); Sabie Gorge, (—BB), *V.A. Wäger* 21 (PRE); on road to Lydenburg, at turnoff to Witklip, Coromandel Farm, at waterfall, (—AB), *Perold & Koekemoer* 2839, 2844 (PRE); Nelspruit Dist., Rooiwal, (—BC), *Bosman* 3180 (PRE); Rosehaugh, (—BD), *T.R. Sim* CH 1286 (PRE); Kaapschoop, (—DB), *H.A. Wäger* 47 (PRE); Berlin State Forest, Kaapschoop hiking trail near Battery Creek, (—DA), *Koekemoer* 973, 975 (PRE).

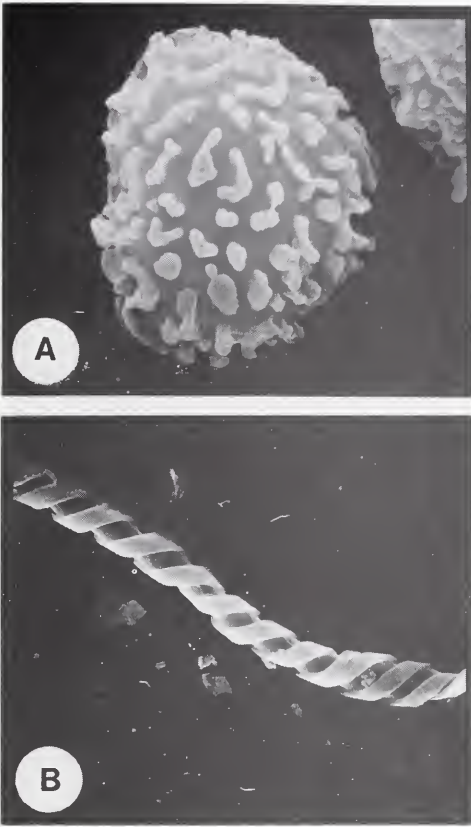


FIGURE 3. — *Dumortiera hirsuta*. A, spore, distal view; B, part of elater. A, B, H. Anderson CH 4527. A, $\times 1730$; B, $\times 480$. SEM micrographs by S.M. Perold.

SWAZILAND. — 2531 (Komatipoort): King Forest, Havelock, occasionally on wet shaded earth bank in forest, (—CC), *Schelpé 6195* (BOL).

NATAL. — 2731 (Louwsburg): Ngoma For., bank of river, (—CD), *Gerstner 4386* (PRE); Ngoma For., Cetshwayo waterfall walk, vertical slope, seepage, in deep shade, (—CD), *Glen 2881* (PRE); Ngoma For., along path in Ntendeka, alongside streams in forest interior, (—CD), *Nicholas 1176* (PRE); Ngoma Forest, occasionally on deeply shaded earth banks in forest, (—CD), *Schelpé 6237* (BOL); Ngoma For., (—CD), *T.R. Sim CH 1302* (PRE); Ngoma For., Ntendeka, in forest, (—CD), *A.E. van Wyk 6973* (PRE). 2828 (Bethlehem): Mont-aux-sources, (—DD), *Doidge 171* (BOL, PRE). 2831 (Nkandla): Nkandla Forest, common on rocks in and near water in shade, (—CA), *Nixon 57* (BOL); Eshowe, Signal Hill, (—CD), *Van der Plank CH 1290, CH 1298* (PRE); Ngoya, (—DC), *T.R. Sim CH 1289* (PRE). 2929 (Underberg): Mpendle Dist., 6 miles along Everglades/Boston Road River on stream bank, in shade, (—DB), *Moll 726* (BOL, PRE); Home Rule, Polela, (—DC), *T.R. Sim CH 1305* (PRE); Xumeni For., (—DD), *Doidge 3581* (PRE); Donnybrook, (—DD), *Scott 3756* (PRE). 2930 (Pietermaritzburg): Karkloof, (—AC), *T.R. Sim CH 1291* (PRE); Buccleugh, (—AD), *T.R. Sim CH 1301* (PRE); Pietermaritzburg, Town Bush, (—CB), *T.R. Sim 7523, 7534*; Waterfall, (—CB), *T.R. Sim 7548, 7574, 7586* (PRE); Pietermaritzburg, (—CB), *T.R. Sim 1296* (PRE); Sweetwater stream, (—CB), *T.R. Sim 1300* (PRE); Zwaartkop, (—CB), *T.R. Sim CH 1328* (PRE).

CAPE. — 3226 (Fort Beaufort): Katberg For., (—BC), *Garabedian S.A.M.H. 49743* (BOL, PRE); Hogsback, (—DB), *T.R. Sim 1895*; *Van der Bijl 176*; *Young 1303* (PRE). 3227 (Stutterheim): Perie Forest, (—CC), *T.R. Sim 7534* (BOL). 3318 (Cape Town): Cape Town, (—CD), *H.A. Wager 28* (PRE). 3322 (Oudtshoorn): Rust en Vrede, at Oudtshoorn, (—CA), ex Herb. C. vanden Berghen (BOL). 3323 (Willowmore): Gouma Forest, near Lily vle, (—CC), *S. Arnell 1736* (BOL); Bloukrans River Pass, at bridge in forest, on rocks along stream, (—DC), *Stirton 9648* (PRE); Bloukrans, along pass in river ravine, on vertical cliff face, (—DC), *Zantovska 155* (PRE). 3419 (Caledon): Oudebos, Rivier-sonder-

end, (—BB), *Thorne 3617* (BOL, PRE). 3420 (Bredasdorp): Leeuwrivier Mountains, Swellendam, (—AB), *Stokoe 9486* (BOL). 3423 (Knysna): Knysna, Garden of Eden, (—AA), *S. Arnell 2096* (BOL); Knysna, (—AA), *T.R. Sim 1292* (PRE).

LUNULARIA Adanson

Lunularia Adanson, Familles des plantes 2: 15 (1763); Micheli: 4 (1729); Nees ab Esenbeck: 29 (1838); Gottsche *et al.*: 510 (1846); Schiffner: 35 (1893); Stephani: 216 (1899); Howe: 59 (1899); Macvicar: 38 (1926); Sim 123 (1926); Müller: 366 (1951–1958); S. Arnell: 73 (1963); Hässel de Menéndez: 125 (1963). Type species: *Lunularia cruciata* (L.) Dum. ex Lindb.

Selenia J. Hill: 120 (1773) nom. illeg.

Staurophora Willd.: 101 (1809).

Dichominum Neck.: 345 (1790) (as subgenus).

Marsilia O. Kuntze 2: 837 (1891).

Sedgwickia S. Bowdich: 35 (1825).

Thallus large, flat, somewhat glossy, green, in overlying patches, sometimes in extensive turfs; on damp soil in old gardens, nurseries and forested areas, may have been introduced into southern Africa. Branches dichotomously furcate toward apex, new growth by apical or lateral innovations; thickened over midrib, gradually thinning toward slightly undulate, hyaline margins; apex emarginate. Dorsal epidermis persistent, hyaline, cell walls sometimes thickened at corners or entirely; air pores simple, elevated and conspicuous, surrounded by several concentric rings of cells, leading below into individual air chambers, these in one layer and floored by chlorophyllous layer of 3–5-celled erect, branched filaments; storage tissue compact, cells colourless, sometimes with pitted walls; scattered cells throughout with single, large, brown oil body; rhizoids numerous, between ventral scales and on midrib, some smooth, others tuberculate; scales ventral, in curved parallel rows on either side of midrib, with round or reniform appendages, several cells containing oil bodies.

Dioicous. *Antheridia* sunken into slightly elevated, oval or kidney-shaped, disciform receptacles encircled by raised, membranous sheath, at sides of male thalli (although originally terminal). *Archegonia* enclosed in terminal receptacles, but by continued growth of thallus

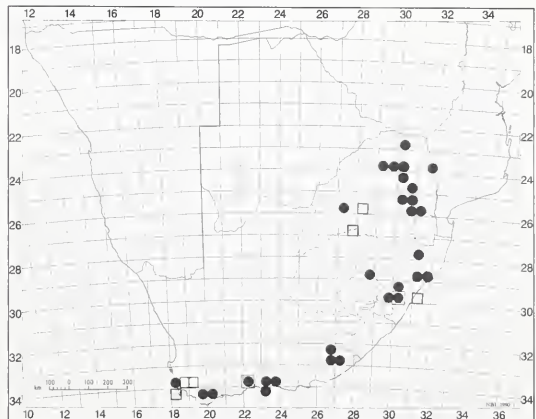


FIGURE 4. — Distribution of *Dumortiera hirsuta*, ●, and *Lunularia cruciata*, □, in southern Africa.

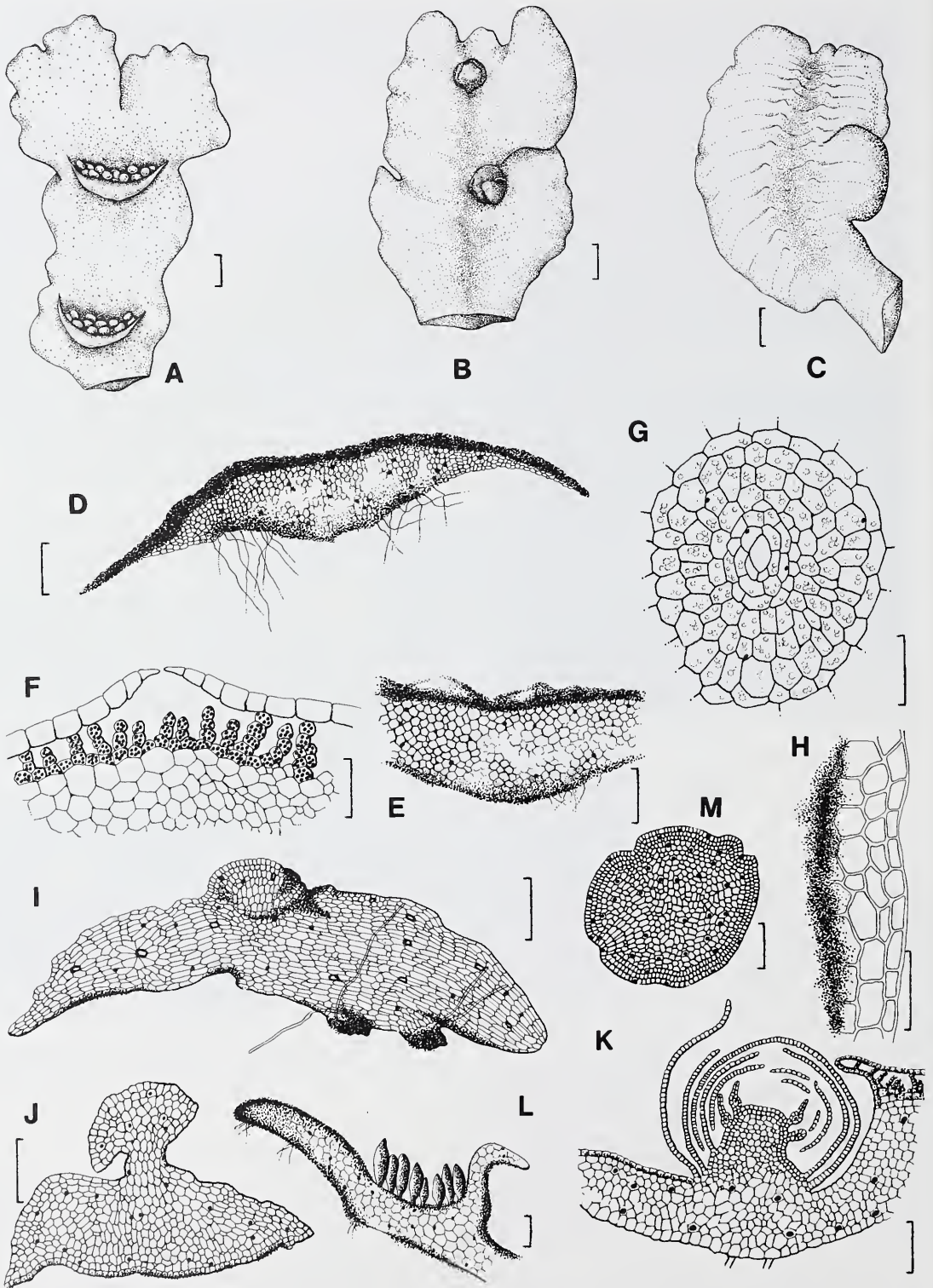


FIGURE 5.—*Lunularia cruciata*. A, dorsal view of thallus with gemma cups; B, female plant with young archegoniophores; C, ventral view of thallus with new lateral branch; D, transverse section of thallus; E, transverse section of midrib region, much enlarged; F, transverse section of air chamber; G, air pore seen from above; H, margin of thallus with hyaline cells, seen from above; I, older scale; J, young scale; K, longitudinal section through young archegoniophore; L, longitudinal section through gemma cup; M, gemma. A, D–H, J, L, M, S.M. Perold 2821; B, C, S.M. Perold 1996. Scale bars: A–C = 2 mm; D, E, K, L = 1 mm; I, J = 500 μm; F, M = 100 μm; G, H = 50 μm. Illustrations by A. Pienaar. Figure 1K partly after Benson-Evans & Hughes fig. 4.

laterally situated, conical, white and bud-like when young, sheathed in layers of scales and slightly sunken into rounded depression with distinct rim; after fertilization and further growth, four tubular involucre in the form of a cross are formed, each enclosing one or two sporophytes, composed of foot, seta and capsule, raised on unfurrowed, hairy stalk; capsules eventually exposed by elongation of seta, the wall unistratose, lacking annular thickenings, dehiscing by 4 valves. *Spores* very small, green or brown, smooth. *Elaters* long, tapering and bispiral. *Gemmae* numerous, disc-shaped, inside crescent-shaped ridge; wholly diagnostic. *Sporophyte* virtually unknown in southern Africa.

***Lunularia cruciata* (L.) Dum. ex Lindberg**, Notiser Sällskap pro Fauna et Flora Fennica Förhandlingar 9: 298 (1868); Howe: 60 (1899); Macvicar: 40 (1926); Sim: 24 (1926); Müller: 366 (1951–1958); S. Arnell: 73 (1963); Hässel de Menéndez: 126 (1963); E.O. Campbell: 31 (1965). Type: In Europae umbrosis [OXF, syn.; H-SOL, isosyn., fide Grolle (1976)]. For detailed synonymy see K. Müller (1951–1958).

Thallus moderately large and flat, ribbon-like or margins somewhat irregular (Figure 5A), glossy, bright green to yellowish green, with outlines of subdorsal air chambers faintly visible from above, each of the polygonal areas with a central air pore, when wet; reticulum indistinct, leathery, when dry; in crowded overlying patches, dichotomously or irregularly furcate or with apical or lateral innovations from ventral side of thallus (Figure 5C). *Branches* 40–55 \times 5–8(–10) mm, \pm 650(–1000) μ m thick over median, ventrally bulging midrib, gradually thinning out laterally into wide wings (Figure 5D); apex emarginate or sinusoidal; margins slightly undulate and somewhat scalloped, with outer 4(5) cell rows hyaline.

Dorsal epidermal cells hyaline, in one layer, 5- or 6-sided to irregular in shape, 35–50 \times 20–30 μ m, thin-walled to somewhat thicker-walled or only thickened at corners, in cross section 20–25 μ m thick; marginal cells with outermost row short- to long-rectangular (Figure 5H), 15–27 \times 10–12 μ m, cells of inner rows polygonal, 17–27 \times 25 μ m; air pores simple, oval, raised, 17–25 \times 12–20 μ m in diameter, bordered by 3–5 rings of curved, smaller, thin-walled cells (Figure 5G), 7–12 \times 17–27 μ m, outer row of cells somewhat larger, 15–20 \times 20–22 μ m; air chambers with domed roof (Figure 5F) raised 37–52 μ m above filaments, laterally separated by non-chlorophyllose unistratose partitions obscured by filaments, floored by dense chlorophyllose layer, \pm 70 μ m thick, of 3–5-celled erect, branched filaments, filled with chloroplasts, top cell often clavate, \pm 20 \times 15 μ m, others 20 \times 12 μ m; midrib below assimilation cells, with \pm 15(–20) rows of compact colourless storage cells (Figure 5E), 50–75 \times 45–50 μ m, becoming smaller ventrally, some with pitted walls, layers gradually decreasing in the wings; scattered cells with brown oil bodies, round or oval, 30 \times 30–45 \times 27 μ m; ventral epidermal cells 30–40 μ m wide, 15–25 μ m thick in cross section; rhizoids on midrib between scales, numerous, smooth, \pm 30 μ m wide, tuberculate, (10–) 17–22 μ m wide. *Scales* hyaline, some basal cells purple, on either side of midrib, stretched across ventral face of wings, near apex of thallus, base \pm 1375 \times 550 μ m, with rounded, constricted appendage (Figure 5J), \pm 400 \times 250

μ m; cells mostly polygonal, \pm 65 \times 25 μ m, some smaller, with oil body 22 \times 25 μ m, almost entirely filling cell; older scales larger (Figure 5I), base up to 1000 \times 4250 μ m, appendage \pm 600 μ m wide.

Dioicous. Male plants quite rare in southern Africa. *Antheridiophore* on alternate sides, having originally developed in terminal sinus near apex (Figure 6A), slightly raised, ovate, flattish discs, 2–3 mm in diameter, encircled by membranous sheath with crenate edges, containing numerous antheridia, individually sunken in flask-shaped cavities (Figure 6B), opening above by pores. *Archegoniophore* originally also developing in terminal sinus near apex, with further growth of thallus leaving it behind, so that it appears lateral in position on alternate sides of thallus (Figure 5B); commences as domed disc \pm 200 \times 375 μ m, bearing several archegonia in radiating rows and attached by very short stalk to floor of shallow, round hollow, 1100 μ m wide \times 300 μ m deep, with crenate rim; sheathed in \pm 3 layers of scales (Figure 5K), outer layer formed by fused, shaped scales, bulging in centre and constricted below and above, upper edge irregularly fringed with filiform cellular appendages of up to 7 rectangular cells, \pm 35 \times 15 μ m, cells in body of scale thick-walled, 5- or 6-sided, up to 57 \times 25 μ m, in between numerous smaller cells, 4- or 5-sided, 25 \times 15 μ m, almost entirely filled with single oil body; between scales and especially from base of archegoniophore and arching over it, numerous uniseriate, long hairs of 16–20 cells each. Further development not recorded as fertilization did not take place, nor are sporophytes available for study. *Gemmae* numerous, disc-shaped (Figure 5M), notched

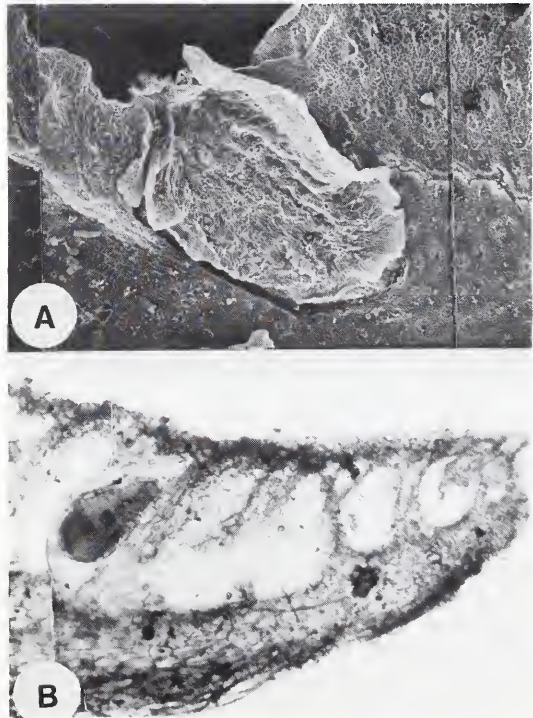


FIGURE 6. —*Lunularia cruciata*. A, antheridiophore seen from above; B, longitudinal section through antheridiophore, with one flask-shaped antheridium in place. A, Wilman BOL. No. 24870; B, Koekemoer 1004. A, \times 22; B, \times 38. A, SEM micrograph; B, LM photograph.

by 2 opposite, lateral growing points, $\pm 430 \mu\text{m}$ in diameter when mature, developing upright on short stalk, inside crescent-shaped cupule (Figure 5L), $\pm 3 \text{ mm}$ wide with crenate to entire ridge on proximal side. *Chromosome number* $n = 8$ (Heitz 1927); $n = 9 = 8 + x/y^2$ (Lorbeer 1934); $n = 9$ (Bornefeld 1987).

DISCUSSION

As mentioned in the description, male plants with anthridial receptacles are exceedingly rare in southern Africa and the only two, *Wilman BOL No. 24870*, on loan from BOL and *Koekemoer 1004* (PRE), were received after completion of Figure 5 and therefore not illustrated there (see Figure 6). Male plants are so rarely seen, that Sim (1926) had categorically stated that they are not present in South Africa, but then added 'so far as is known'. He must have been unaware of Saxton's find. No female plants with fertilized archegonia and mature sporophytes were available for study; even plants with young archegoniophores are quite rare, judging both from personal experience and from the literature (Saxton 1931; Goodman 1956; E.O. Campbell 1965). Saxton (1931) found both male and female plants in Cape Town in 1908, but had to wait for almost 20 years for plants with mature archegoniophores (forwarded from Dartmouth, England) to complete his studies on the life history of *L. cruciata*. Giffen sent plants with young archegoniophores from Oranjezicht, Cape Town to Sim (Sim 1926) and Auret (as mentioned in Benson-Evans & Hughes 1954) reported the regular production of female branches in the vicinity of Johannesburg. Of my own collections, only *S.M. Perold 1996* from Devon Valley Hotel, Stellenbosch (November 1987), had young archegoniophores.

Since so many collections are from nurseries or city gardens, it would appear that *L. cruciata* may have been introduced into southern Africa. It is not frequently found here, most collections being from the southwestern Cape, a few from southern Transvaal and some from Natal, and then quite frequently from nurseries (Figure 4). Further north in Africa, *L. cruciata* is known from Zimbabwe (Best 1990), Malawi (Nyika Plateau, *S.M. Perold 2667*, 2676 (PRE)); East African Mountains (Arnell 1956); Tanzania (Serengeti) (Vanden Berghen 1965); Uluguru Mountains, Rungwe Mountains (Bizot & Pócs 1979); Congo Rep. (Katanga) (Vanden Berghen 1965). Pócs (pers. comm.) states that in East Africa, *L. cruciata* is found in many natural habitats in the montane forest belt, mostly on young volcanoes such as Mt Elgon and Mt Meru and even on the Comoro Islands.

Lunularia cruciata is quite widespread in the southern hemisphere but regarded by Engel & Schuster (1982) as probably Laurasian in origin. Since sexual reproduction and subsequent spore production are so rare, its gemmae obviously present a highly effective means of ensuring its dispersal, which is most likely aided by human activities.

On the basis of its flavonoid chemistry, Campbell *et al.* (1979), include it in the Marchantiaceae, but in the present treatment Grolle (1983) is followed and *L. cruciata* is classified in the monotypic family, Lunulariaceae Klinggr. (1858).

Its phylogenetic position seems rather unclear, Schuster (1984b) arguing that he would place it 'low' in the Marchantiales on account of its high level of seta retention, 2–3 sporophytes per gynoeceum and a capsula with 4 well-defined valves. On the other hand, he expresses the viewpoint (Schuster 1984b) that its archegoniophore, clearly formed from two dichotomies, each producing archegonia, is complex and therefore an advanced feature.

SPECIMENS EXAMINED

TRANSVAAL. —2528 (Pretoria): Pretoria, Union Buildings Nurseries, (–CA), *Bottomley CH 135* (PRE); Pretoria, National Botanical Institute Nurseries, (–CA), *S.M. Perold 2821* (PRE). 2627 (Potchefstroom), Vereeniging, (–DB), *T.R. Sim CH 1283* (PRE); Roodepoort, Sterlig Nursery, on gravel and brick walls of flowerbeds, (–DD), *Koekemoer 1004* (PRE).

NATAL. —2930 (Pietermaritzburg): Hilton Road, (–CB), *T.R. Sim CH 1279*, *CH 1280* (PRE). 2931 (Stanger): Durban, Silverglen Nurseries, (–CC), *S.M. Perold 2805* (PRE).

CAPE. —3318 (Cape Town): Kirstenbosch, (–CD), *S. Arnell 412* (BOL); Window Gorge, Table Mountain, (–CD), *S. Arnell 405* (BOL); Claremont Park, (–CD), *Garside 6653* (BOL); near Round House, (–CD), *Garside 6132* (BOL); Oranjezicht, (–CD), *Giffen CH 1281* (PRE); Glen Picnic Resort, just below Round House, Lion's Head, (–CD), *S.M. Perold 645* (PRE); Round House, Lion's Head, on soil beneath trees, (–CD), *S.M. Perold 650* (PRE); Newlands Forest, on soil under trees, (–CD), *S.M. Perold 662* (PRE); Cape Town, (–CD), *T.R. Sim CH 1278*, *CH 1282* (PRE); Skeleton Gorge, rock face, very wet forest, (–CD), *Stirton 9415* (PRE); mountain slopes above Kirstenbosch, (–CD), *Stokoe s.n.* (BOL); Kirstenbosch, (–CD), *Wilman 24870* (BOL); Stellenbosch, (–DD), *Burt Davy CH 1277* (PRE); Pniel, on tree trunk mixed with moss, (–DD), *Morley 314* (PRE); Stellenbosch, Devon Valley Hotel at garden fence, on soil, (–DD), *S.M. Perold 1990* (PRE); Stellenbosch, Devon Valley Hotel, on soil bank behind hotel, (–DD), *S.M. Perold 1996* (PRE); Stellenbosch, (–DD), *T.R. Sim CH 1284* (PRE); S Paarl, Landskroon, in kloof, (–DD), *Volk 81/071* (BOL, PRE). 3319 (Worcester): W of Franschhoek, Waterval Farm, on earth bank, ditch next to dirt road, (–CC), *S.M. Perold 633* (PRE); 4 km N of Villiersdorp, Elandsriver Road, Du Toitsberge, near waterfall on Sneekop, (–CD), *S.M. Perold 623* (PRE). 3322 (Oudtshoorn): George, NE of Hawthorndene Hotel, at roadside on side of earth water furrow, (–CD), *S.M. Perold 920* (PRE). 3418 (Simonstown): Constantia, on soil on damp rock face, (–AB), *S.M. Perold 656* (PRE).

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Panicum simulans (Paniceae, Poaceae), a new species from southern Africa and its leaf anatomy

L. SMOOK* and R.P. ELLIS**

Keywords: leaf anatomy, morphology, Namibia, new species, *Panicum*, Poaceae

ABSTRACT

Panicum simulans Smook from northern Namibia is formally described. The morphology and leaf blade anatomy in transection and surface view, as observed under the light microscope, are described. The species is compared to others with which it has been confused in the past. *P. simulans* can be readily distinguished from *P. novemnerve* Stapf and *P. schinzii* Hack. on the basis of both anatomical and morphological characters such as the venation of the lower glume and the photosynthetic anatomy, which is of the NAD-me subtype of the C_4 photosynthetic pathway. On this basis it appears that *P. simulans* is closely allied to the *P. coloratum* L. group of species and should be placed in section *Panicum* of subgenus *Panicum*.

UITTREKSEL

Panicum simulans Smook vanaf die noordelike Namibië word formeel beskryf. Die morfologie en blaaranatomic, in deursnee en oppervlakaansig, soos met die ligmikroskoop waargeneem, word beskryf. Die morfologie en blaaranatomic van *P. simulans* word vergelyk met dié van twee ander spesies wat verwarring in die verlede geskep het. *P. simulans* kan maklik van *P. novemnerve* Stapf en *P. schinzii* Hack. onderskei word op grond van die bearing van die onderste gluma en die fotosintetiese anatomie wat van die NAD-me sub tipe van die C_4 -fotosintetiese weg is. Op grond van hierdie gegewens word *P. simulans* in die seksie *Panicum* van subgenus *Panicum* geplaas.

Panicum simulans Smook, sp. nov.

Panicum sp. 2 (Giess 8605) in Gibbs Russell *et al.*: 242 (1990).

Panicum spp. in Group 3a in Ellis (1988).

Panicum simulans Smook, sp. nov., *P. novemnervi* Stapf similis sed gluma inferiori uninervi, flosculo inferiori masculo, paleaque inferiori bene evoluta differt; *P. schinzii* Hack. similis sed nodis culmorum adpresso-hirsutis, apicibus glumae superioris et lemmae inferioris erectis vel recurvis, atque chloroplastis centripetis, non centrifugis, differt.

Annual. Plant variable; usually yellowish green in colour, often flushed purple. Culms erect to geniculate, 600(–1 200) mm high (from plant base to top of inflorescence); sometimes rooting at nodes; nodes with adpressed silvery white hairs pointing upwards; base covered with leaf sheaths; internodes usually not visible. Leaf sheaths glabrous or with bulbous-based hairs varying in length and size of hair and relative size of base. Ligule a fringed membrane 1.4 mm long (membranous rim 0.3 mm, cilia 1.1 mm long). Leaf blade linear, 5–200(–250) × 2–15 mm, straight or cordate at base, flat, many-nerved, bulbous-based hairs present or absent; apex acute to acuminate; margins white, smooth to scaberulous to densely scabrid; adaxial surface densely papillate especially on lower leaves; nerves of abaxial leaf surface smooth, occasionally densely scabrid especially near leaf apex (variable on same plant).

Inflorescence a panicle (80–)160–250(–400) mm long, narrowly obovate to obovate, occasionally oblanceolate, sometimes asymmetrical (lowest branch longest, protruding beyond other branches), moderately branched, usually ascending and spreading; lowest branches single or a number arising from same side, not whorled; next set of branches often whorled or in a pseudo-whorl; branches naked for a long way up from base with spikelets crowded at apices, smaller branches usually scabrid with prickles becoming denser, longer and larger towards spikelets; spikelets usually in pairs on long-short pedicels on branchlets. Spikelets narrowly obovate to obovate-elliptic, (2.2–)2.4–2.6(–3.0) mm long, acute to acuminate, often flushed purple. Lower glume broadly ovate, $\frac{1}{3}$ to just over $\frac{1}{2}$ as long as intact spikelet, clasping base of spikelet, membranous; central nerve distinct, often scaberulous to scabrid; lateral nerves obscure, if present, only visible at base; apex acute to acuminate, sometimes minutely mucronate or with a brush of prickles. Rachilla pronounced between glumes. Upper glume 2.4–2.6(–3.0) mm long, longer than lower lemma, membranous, 7–9(11)-nerved (nerves nearest margins sometimes obscure and short); central nerve thickened at apex, forming a usually scabrid mucro; apex acute to acuminate, either erect or slightly recurved outwards; margins below apex membranous and folding inwards, often flushed purple and then mainly at apex. Lower floret male only; anthers 3, developed 1.4–1.7 mm long or rudimentary, both conditions present on same inflorescence, dark orange-brown. Lower lemma similar to, but shorter than upper glume, fitting into its apex, (7–)9-nerved; cross venation often visible; central nerve scaberulous, thickened towards apex; apex acute to truncate; margins broad and membranous, either folded in or out, often purple especially near apex. Lower palea well developed, nearly as long and as wide as lower lemma. Upper lemma and palea smooth, shiny, pale, white to straw-coloured, occasionally dark with

* National Botanical Institute, Private Bag X101, Pretoria 0001.

** Agricultural Research Council, Roodeplaat Grassland Institute, Private Bag X05, Lynne East, Pretoria 0039.

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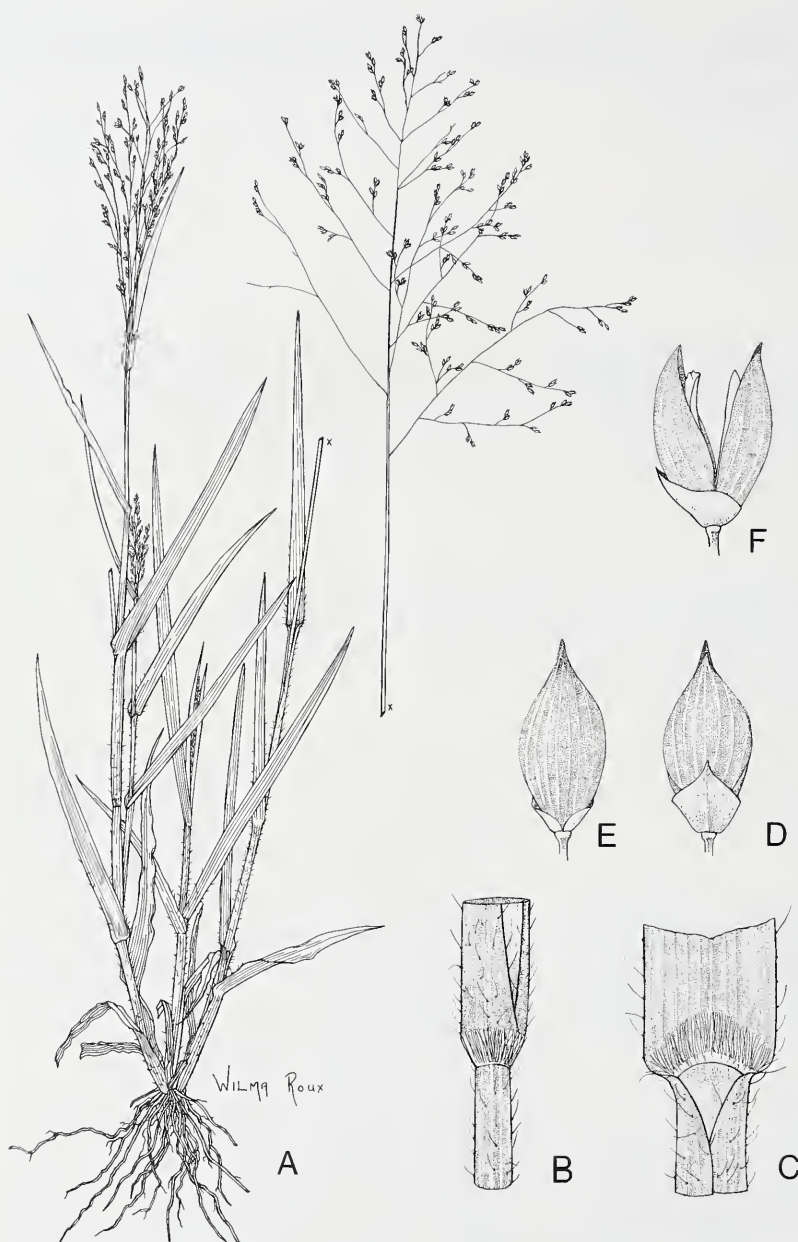


FIGURE 1.—*Panicum simulans*. A, habit, $\times 0.5$; B, node showing adpressed hairs, $\times 2.5$; C, ligule, $\times 2.5$; D, spikelet showing lower glume, $\times 10$; E, spikelet showing upper glume, $\times 10$; F, lateral view of open spikelet, $\times 10$. From Smook 5108 and Giess 8605.

distinct yellow nerves on upper lemma, both colour forms sometimes present on same plant. *Styles* 2, separate; stigmas plumose, purple to dark brown (on herbarium specimens). Figure 1.

TYPE.—Namibia, 1915 (Otjihorongo): 25 km N of Outjo on road to Okaukuejo, (—DD), Smook 5108 (PRE, holo.) (Smook 5108a, PRE, isotype*).

Panicum simulans has been confused with *P. schinzii* Hack. and *P. novemnerve* Stapf in the past, and the specimens now included in this new species have been misidentified as either of these two species. However, this study shows that several characters serve to separate these

three species clearly and to justify the recognition of *P. simulans* (Table 1). The specific epithet refers to the superficial similarity between *P. simulans*, *P. schinzii* and *P. novemnerve*.

Figure 2 shows the known distribution of *P. simulans*. It is restricted to northern Namibia but may possibly also occur in southern Angola. It is associated with various vegetation types ranging from mopane woodland to mopane mixed with *Acacia*, *Combretum* or *Terminalia* to sweet grassland on limestone soils such as occur around Etosha Pan.

Panicum simulans is hydrophytic and grows typically in areas with seasonally high moisture regimes as found in vleis and around fountains. It may even occur in more

* This is the anatomical voucher specimen.

TABLE 1.—Comparison between *Panicum novemnerve*, *P. simulans* and *P. schinzii*

	<i>novemnerve</i>	<i>simulans</i>	<i>schinzii</i>
culm nodes	adpressed hairy	adpressed hairy	glabrous
lower glume venation (distinct)	3–5-nerved	1-nerved	1-nerved
apex of upper glume and lower lemma	erect or recurved	erect or recurved	folded inwards
lower floret	sterile	male	male
lower palea	reduced	well developed	well developed
Kranz chloroplasts	centripetal	centripetal	centrifugal

ephemerally moist situations such as in depressions in disturbed situations along roadsides or irrigated lands or in natural hollows in granite outcrops or saturated soil pockets overlying calcrete.

Specimens examined

NAMIBIA. —1713 (Swartbooisdrift): Kaokoveld, (–DD), *Merxmüller & Giess 35538*, 1813 (Ohopoho): Kaokoveld, (–BB), *De Winter & Leister 5160*, 1815 (Okahakana): Etosha National Game Park, (–DC), *Le Roux 1399*, 1817 (Tsietsabis): 56 km S of Namutoni on road to Tsumeb, (–CD), *Smook 5153**; Farm Falkenhain GR/TS 303, (–DA), *Giess 15090*, 1914 (Kamanjab): 15 km N of Otjovasandu, (–AB), *Giess 9253*; Farm Grootberg, (–CD), *Du Toit 236*, 1915 (Okaukuejo): Etosha National Game Park, Vogelnestvlei, (–BB), *Giess & Mueller 13971*, 10 km S of Okaukuejo, *Giess & Louit 14143*; 9 km E of Okaukuejo, *Smook 5109**, (–BB), *Tinley 12994*; Ombika, (–BD), *Le Roux 328*; Ombika detour, *Giess & Louit 14113*; near Ombika, *Giess 15078*; 25 km N of Outjo on road to Okaukuejo, (–DD), *Smook 5108**, 1916 (Gobaub): Etosha National Game Park, Olifantsbad, (–AA), *Ellis 5271**, *5273**; Gemsbokvlakte, (–AA), *Smook 5110**; Halali, (–BA), *Van der Westhuizen 23*, 1917 (Tsumeb): Tsumeb, (–BA), *Giess 8605*, 1918 (Grootfontein): Farm Sus, (–AB), *Schweickerdt 2144*, 2015 (Otjihorongo): Farm Pamela, (–AB), *Volk 2855*; Farm Babatsi, (–AB), *Gibbs Russell & Smook 5628**; Farm Straussenheim OUT 133, (–BB), *Giess, Volk & Bleissner 6004*, 2115 (Karibib): Farm Etimba, (–BC), *Giess 10799*; Farm Schlucht OM 162, (–DA), *Giess 8435*; Farm Ameib, *Giess, Volk & Bleissner 5898*, *De Winter & Hardy 8072*.

LEAF ANATOMY OF *PANICUM SIMULANS*

In order to obtain further evidence relating to the taxonomic status and position of *P. simulans*, a detailed anatomical study was undertaken. The methods used are described in Ellis (1988) and the terminology used is defined in Ellis (1976 & 1979). The following abbreviations will be used:

- vb/s = vascular bundle(s)
- 1'vb/s = first-order vascular bundle(s)
- 2'vb/s = second-order vascular bundle(s)
- 3'vb/s = third-order vascular bundle(s)
- ibs = inner or mestome sheath
- obs = outer or parenchyma sheath

Leaf blade in transverse section

Outline: expanded blade, flat to very broadly V-shaped; arms of lamina straight or gently undulating; blade symmetrical about midrib. *Ribs and furrows*: shallow and wide adaxial furrows present between all vbs; slight,

rounded ribs occur in association with all vbs; similar ribs occur over all vbs. No abaxial ribs or furrows present. *Median vascular bundle*: variable, either median bundle only present (this indistinguishable structurally from lateral 1'vbs and without additional parenchyma tissue) (Figure 3A) or keel with associated colourless parenchyma tissue present (Figure 3B); 1, 3 or 5 vbs incorporated in keel; all bundles abaxially located; larger keels rounded with single adaxial groove; no adaxial sclerenchyma developed and abaxial girders associated with all vbs; no air spaces in keel. *Vascular bundle arrangement*: 5, 7, 9 or 11 1'vbs in transection; 3, 4 or 5 3'vbs between consecutive 1'vbs; narrower leaves without keels, with 5 1'vbs and with three 3'vbs between successive larger bundles. No 2'vbs. All vbs situated in centre of blade. *Vascular bundle description*: 3'vbs circular in outline with xylem and phloem distinguishable. 1'vbs circular in shape, lysigenous cavities present (Figure 3E, F) and metaxylem vessels narrow (diameters less than those of obs cells) and circular. *Vascular bundle sheaths*: obs conspicuous, round, entire (except with small abaxial interruption in 1'vbs) and without extensions; consists of 6, 7 or 8 cells around 3'vbs and 11–14 cells around 1'vbs; obs cells fan-shaped with radial walls straight and outer tangential walls inflated (Figure 3E, F); all cells similar in size and shape; chloroplasts dense, filling entire cell lumen or concentrated centripetally, near inner tangential wall. Ibs absent in 3'vbs; complete but inconspicuous in 1'vbs; cells very much smaller than obs cells; adaxial cells slightly larger and thin-walled; lateral and abaxial cells uniformly thickened but degree of secondary thickening very variable. *Sclerenchyma*: minute adaxial and abaxial strands only associated with 1'vbs; no fibrous tissue in association with 3'vbs. Small sclerenchyma caps in leaf margin (Figure 3A). *Chlorenchyma*: distinctly radiate; single layer of tabular cells completely surrounds all vbs (except sometimes for a short abaxial interruption with 1'vbs); radiating chlorenchyma of successive bundles in direct contact and not separated by colourless parenchyma. No colourless parenchyma tissue present (except in midrib, if present). *Adaxial epidermal cells*: bulliform cells small, in rather extensive groups; central bulliform cell occupies less than 1/4 of leaf thickness; cuticle very thin; no macrohairs, except rarely in association with margin; no prickles or hooks evident; cuticular papillae common, much narrower than epidermal cells and with one per cell as seen in

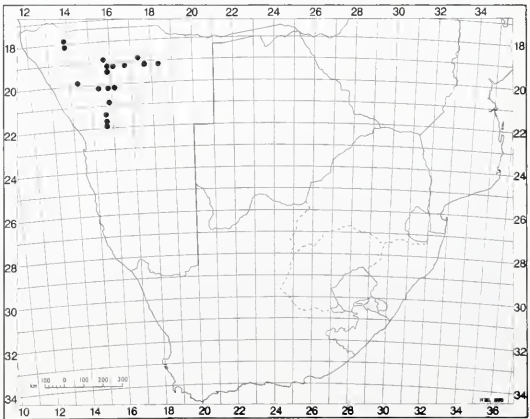


FIGURE 2.—The known distribution of *Panicum simulans*.

* voucher specimens for anatomical study.

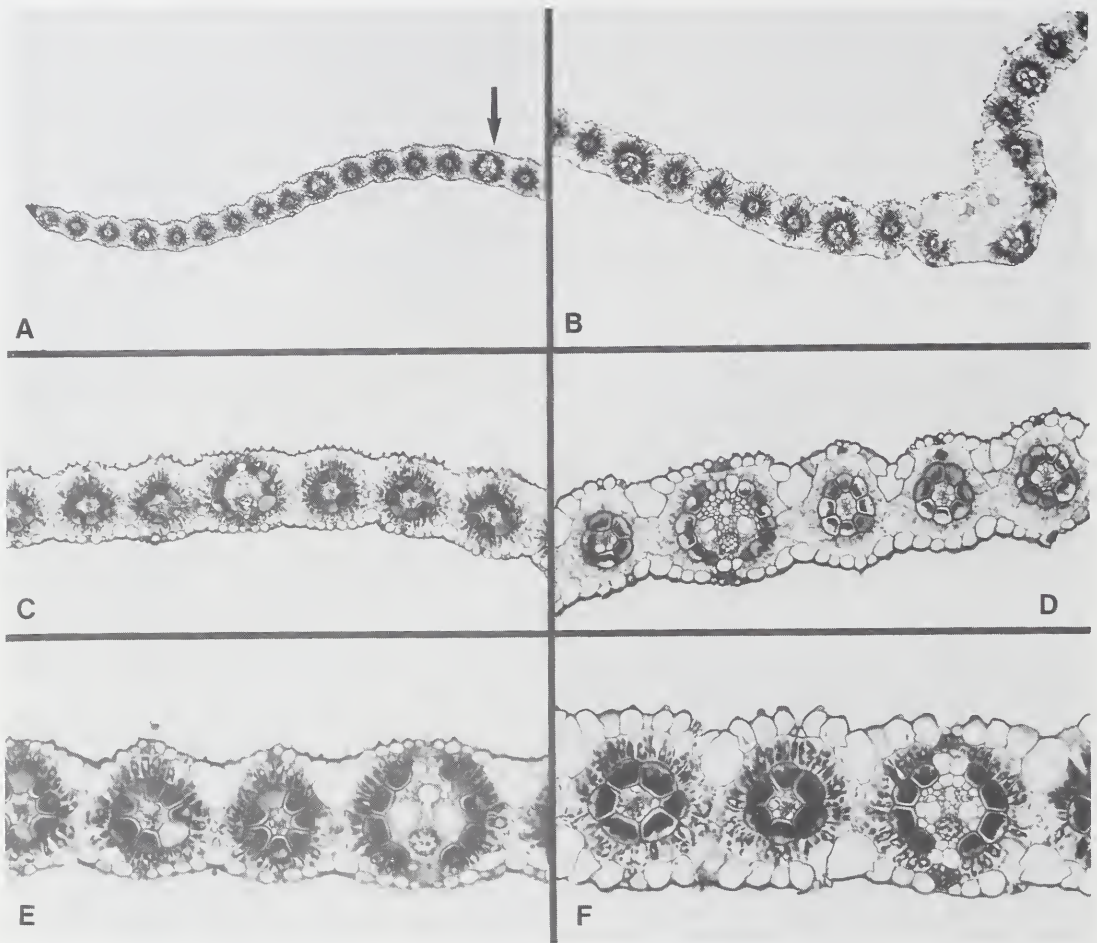


FIGURE 3. —Leaf blade anatomy of *Panicum simulans* as seen in transverse section. A, outline of specimen without keel; median vascular bundle only (arrowed), this bundle structurally indistinguishable from other first-order vascular bundles; B, outline of specimen with distinct keel incorporating four vascular bundles and adaxial colourless parenchyma tissue; C, typical C_4 photosynthetic anatomy with prominent parenchyma sheaths; D, specimen showing distinct centripetal location of Kranz chloroplasts in outer bundle sheath cells; E, dense chloroplasts in outer bundle sheath cells and radiate chlorenchyma, note adaxial papillae; F, typical NAD-me type photosynthetic anatomy. A, B, $\times 100$; C, D, $\times 250$; E, F, $\times 400$. A, C, Smook 5108; B, Smook 5120; D, Gibbs Russell & Smook 5268; E, Smook 5153; F, Smook 5110.

section (Figure 3C–F). Abaxial epidermal cells: central cells of intercostal zones larger and resemble bulliform cells in transection; cuticle thin; no macrohairs, prickles or papillae.

Abaxial epidermis in surface view

Zonation: evident but costal zones overlying 3'vbs often without silica bodies as a result of absence of sclerenchyma strands in association with these bundles. **Intercostal long cells:** elongated (length more than $3 \times$ longer than width), side walls parallel to outwardly bowed, end walls vertical; anticlinal walls very thin and slightly undulating, with degree of sinuosity varying with plane of focus; cell shape varies across individual intercostal zones with two files of bulliform-like cells per intercostal zone; these bulliform-like cells actually represent central files of two intercostal zones but costal zones are poorly differentiated (Figure 4C, D). Very few tall and narrow short cells present. **Stomata:** 2 or 4 files of low dome-shaped stomata per intercostal zone; usually separated by a single elongated

interstomatal cell. **Papillae:** absent. **Prickles:** absent. **Microhairs:** bicellular with dehiscent distal cell; only basal cells remain, basal cell elongated with length much greater than width; occur in central files of intercostal zones (Figure 4D). **Macrohairs:** absent. **Silica bodies:** very irregular dumbbell-shaped; horizontally elongated; same width as adjacent long cells. **Costal short cells:** 1 or 3 files of cells comprise costal zones; central file with silica bodies, these alternate irregularly with short to long short cells. Costal zones often not associated with 3'vbs, only present over 1'vbs.

DISCUSSION

In general appearance *P. simulans* closely resembles *P. schinzii*, particularly those forms of both taxa that have rounded or cordate leaf bases. However, the hairy nodes (Figure 1B) and pointed apex of the spikelets (Figure 1D, E) and colour of plant (yellowish green vs. green) of *P. simulans* clearly separate these two taxa (Table 1) (Gibbs Russell *et al.* 1990).

All specimens from Namibia previously assigned to *P. schinzii* have now been re-identified as *P. simulans*. There is one exception, Völk 2672. However, there is no habitat information for this specimen, and it may have been a weed from a cultivated land and imported with the crop.

Panicum schinzii and *P. simulans* both tend to be hydrophytic, but they are clearly separated geographically. Their natural populations were undoubtedly originally allopatric, but it can be expected that, with increasing agriculture under irrigation, *P. schinzii* will become established in the range of *P. simulans*.

In addition to the morphological differences between *Panicum simulans* and *P. schinzii*, there are major differences in the photosynthetic leaf anatomy between these two taxa. *P. simulans* has the NAD-me subtype of the C₄ photosynthetic pathway, as the anatomy is Kranz with a double bundle sheath with the specialized chloroplasts of the parenchyma sheath centripetally arranged (Ellis 1988). The *Panicum* species with this type of photosynthetic anatomy constitute the 'true' *Panicum* species (Brown 1977) as *P. miliaceum* L., the type of the genus, belongs to this group.

Panicum schinzii, on the other hand, characteristically has the Kranz chloroplasts located against the outer tangential cell wall. These chloroplasts are relatively small and often form only a thin peripheral layer in contrast to the large, dense chloroplasts of *P. simulans*. The anatomy of *P. schinzii* is typical of that of the PEP-ck subtype of the C₄ pathway (Ellis 1988). Brown (1977) considered all the *Panicum* species of this PEP-ck subtype, as doubtful

members of the genus and as belonging to *Brachiaria*, together with *Urochloa* and *Eriochloa*. This applies particularly to those species with rugose lemmas.

Ellis (1988) grouped *Panicum simulans* and *P. schinzii* in two different subgeneric groups because of these distinct anatomical differences. *P. schinzii* was placed in Group 2d whereas *P. simulans* (as *Panicum* spp., together with *P. novemnerve*) was placed in Group 3b.

Group 2, although the leaf anatomy is typically PEP-ck throughout, actually consists of two distinct and separate groups. Group 2d with *P. schinzii*, together with *P. gilvum* Launert, *P. impeditum* Launert, *P. repens* L. and *P. subalbidum* Kunth, are all hydrophytic and have pale, glossy upper lemmas. These taxa are clearly not closely allied to Groups 2a–2c, all of which appear to belong to the panicoid grasses with rugose lemmas. The *P. schinzii* group of species (except *P. repens*) belongs to section *Dichotomisflora* (Hitchc. & Chase) Honda of subgenus *Panicum* (Zuloaga 1987) and is not closely allied to *P. simulans* despite the superficial morphological resemblance.

The work of Ohusigi *et al.* (1982) urges caution in assigning *P. schinzii* and its allies to the PEP-ck photosynthetic subtype as they may actually all be NAD-me. The biochemical typification of these taxa urgently needs verification before final taxonomic decisions can be made. However, this has no bearing on the separation of *P. simulans* from this group.

In the past *P. novemnerve* has also been confused with *P. simulans*. However, *P. simulans* has only one distinct

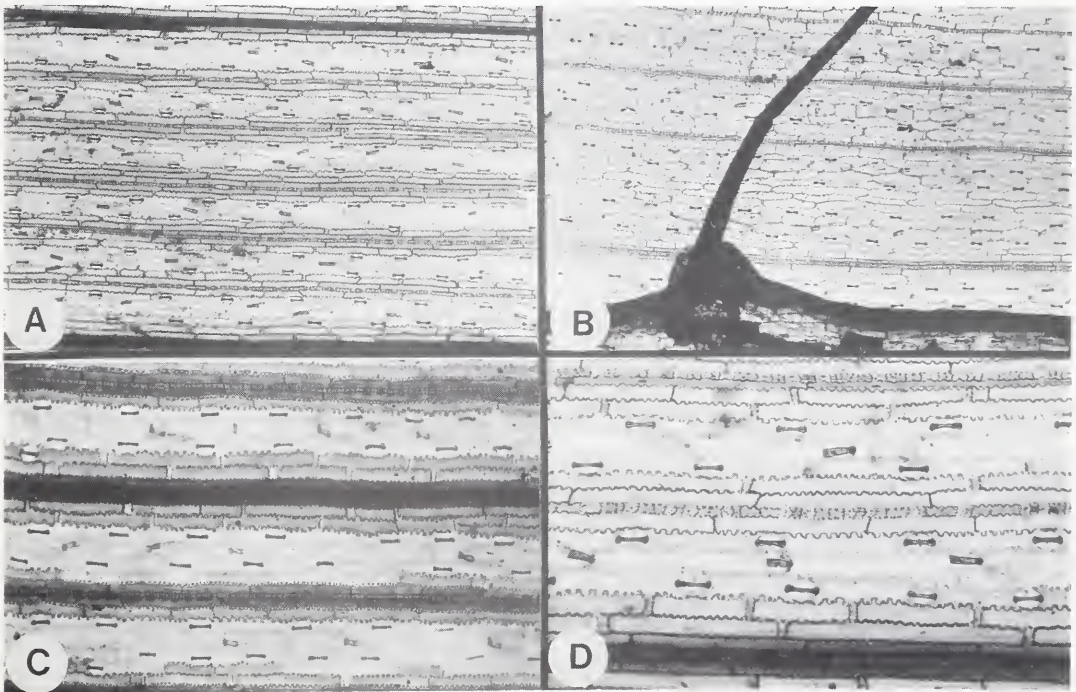


FIGURE 4.—Abaxial epidermal structure of *Panicum simulans*. A, typical zonation pattern with 5 narrow costal zones located over third-order bundles between successive first-order bundles; B, leaf margin showing cushion-based macrohair; C, stomata and microhairs in intercostal zones; D, low dome-shaped stomatal subsidiary cells, basal cells of microhairs and very irregularly dumbbell-shaped silica bodies. A, B, $\times 160$; C, $\times 250$; D, $\times 400$. A, D, Smook 5153; B, Smook 5110; C, Smook 5109.

and obvious nerve on the lower glume (Figure 1D) instead of 3–5 as in *P. novemnerve*. In *P. novemnerve* the lower floret is sterile with a reduced palea (Stapf 1920), whereas in *P. simulans* the lower floret is male with a well-developed palea (Gibbs Russell *et al.* 1990). These two taxa can, therefore, be readily separated on morphological criteria.

Panicum simulans and *P. novemnerve* also share similar damp habitats although *P. novemnerve* appears to prefer shady areas. They are sympatric in Namibia, but *P. novemnerve* also occurs in Botswana and the Transvaal.

The leaf anatomy of *P. novemnerve* (as based on Smook 5163 and Gibbs Russell & Smook 5235) and *P. simulans* is virtually identical. Both have the NAD-me type anatomy with very little sclerenchyma development. The only discernible difference appears to be that the intercostal long cells in *P. novemnerve* are often separated by tall and narrow short cork cells, which is very seldom the case in *P. simulans*. Both *P. simulans* and *P. novemnerve* specimens were included under *Panicum* spp. of Group 3a by Ellis (1988) because of this similarity in leaf blade anatomy. These two annual species, together with *P. arcuameum* Stapf and *P. atosanguineum* A. Rich., undoubtedly belong to the *P. coloratum* L. group of species, and show very close similarities with *P. pilgerianum* (Schweick.) Clayton [= *Psilochloa pilgeriana* (Schweick.) Launert], another annual hydrophyte. This latter species has only recently been placed in *Panicum*, and this small group of annual species appears to form a clear subgrouping within the *P. coloratum* group of species. They resemble an unnamed perennial entity within

P. coloratum particularly closely, as discussed by Ellis (1988). Specimens of this taxon are Ellis 1783, 2905 and 2912, all of which are also hydrophytes. *Oryzidium barnardii* C.E. Hubb. & Schweick., may also belong to this assemblage.

Panicum simulans, therefore, appears to belong with the 'true' *Panicum* species of section *Panicum* of subgenus *Panicum* (Zuloaga 1987). These are typical NAD-me species as suggested by the leaf anatomy but biochemical typing is required.

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Notes on African plants

VARIOUS AUTHORS

ROSACEAE

OBSERVATIONS ON *CLIFFORTIA MICRANTHA*

A fresh specimen of a *Cliffortia* species from the Swartberg (*Vlok 2113*) clearly showed more than one style and, following Weimarck's (1934, 1948) keys, was identified as *C. propinqua* Eckl. & Zeyh. (subgenus *Digraphidium* section *Complanatae*), but its appearance differed greatly from that species. It did, however, match *C. micrantha* Weim. (subgenus *Monographidium*, section *Costatae* or *Bacciformes*; see below) a single-styled species, both in appearance and by key except for the number of styles. With the handling of the fresh specimen, it was clear that the styles were easily shed. A re-evaluation of existing herbarium collections of *C. micrantha* seemed, therefore, necessary. In 15 herbarium specimens examined from three major Cape herbaria (BOL, NBG, STE), two-styled fruits were found occasionally on only five of the specimens; most fruits had no styles and a few only one. The fresh specimen (*Vlok 2113*) was predominantly two-styled with only a few three-styled fruits.

According to Weimarck (1934, 1948), the number of styles and achenes correspond. It should therefore be feasible to count the achenes instead of the styles.

The number of achenes in at least two fruits per specimen, were counted for the 15 specimens of *C. micrantha*. The fruits of the fresh Swartberg specimen (*Vlok 2113*) were also examined for number of achenes. *Esterhuysen* 28523, identified by the collector as *C. micrantha*, but possibly of hybrid origin (see below), was also examined.

All the fruits of *C. micrantha* proper contained at least two achenes. A single specimen from near Prince Albert (*Bond 1680*) had two to three achenes per fruit. A specimen from Noukloof Nature Reserve (*Laidler 154*) had two to four achenes per fruit as well as two styles on some of the fruits. The Swartberg specimen (*Vlok 2113*) had two to three achenes corresponding with the number of styles (Figure 1A–E). The fruit of *Esterhuysen* 28523 appeared more oblong and furrowed than the norm for *C. micrantha* and contained only one achene. Closer examination showed this specimen to differ from *C. micrantha* in the shape and size of the leaves as well, tending towards the characters found in *C. cervicornu* Weim. (Weimarck 1959).

If it is accepted that one style concurs with one achene and two (or more) styles with two (or more) achenes consistently enough to subdivide a genus (Weimarck 1934, 1948), then *C. micrantha* must be regarded as a multiple-styled species because there were never less than two achenes per fruit in all the specimens examined. This is confirmed by the fresh Swartberg specimen (*Vlok 2113*) which has two to three styles and two to three achenes.

Weimarck's (1934, 1948) perception of *C. micrantha* as having a single style could be due to the fact that the styles

in his material had been shed. As he equated the number of achenes to the number of styles, it is most likely that he did not examine the achenes in this species.

Weimarck (1940) placed *C. micrantha* in the section *Costatae* with *C. serpyllifolia* Cham. & Schlecht. and *C. browniana* Burt Davy on the basis of its ribbed fruits and the mistaken assumption that it has a single style. *C. micrantha* can, however, have ribbed or smooth fruits, depending on the age of the fruit, (Figure 1A, F & G) and was therefore placed in two divisions in his key for the section *Costatae* (Weimarck 1948). In the same article, he placed *C. micrantha* in his key for the section *Bacciformes* as well (Weimarck 1948). He discussed it under the latter section which contains only one other species, *C. baccans* Harv. This latter species has a smooth and berry-like fruit, resembling the mature fruit of *C. micrantha*, but with only one style. If *C. micrantha* is retained in either the sections *Bacciformes* or *Costatae*, the number of styles loses its taxonomic importance. Furthermore, the feasibility of subdividing the genus into subgenera on this basis becomes questionable.

On the above evidence, *C. micrantha* should be placed in the subgenus *Digraphidium* on the basis of the predominance of two-styled flowers. This placement is further substantiated by the trifoliate leaves, the tetramerous flowers and the low stamen count common in this subgenus. However, fruits of the only section (*Complanatae*) of this subgenus are flattened and hard, and not berry-like as are the mature fruits of *C. micrantha* (Figure 1A). The older fruits, however, can appear ribbed and the two-achened ones are dorsiventrally flattened, to some extent resembling the fruits in the section *Complanatae* (Figure 1F & G). *C. micrantha* might therefore be placed in the subgenus *Digraphidium* but in its own section. This needs further investigation.

The possible occurrence of more than two styles and achenes in the recognised two-styled species of *Cliffortia* also needs investigation.

The probability of the specimen *Esterhuysen* 28523 being a hybrid between *C. micrantha*, a two-styled species, and *C. cervicornu* Weim., a one-styled species, raises more questions about relationships. A field trip to collect fresh material of this probable hybrid was unsuccessful, but needs to be done again as part of further work on hybridisation and relationships in the genus.

SPECIMENS EXAMINED

For number of styles

CAPE.—3320 (Montagu): Touwsberg, in kloof, S slope near top, 1 100 m, 11-07-1941, (—DB), *Levyus* 7483 (NBG). 3321 (Ladismith): Swart-

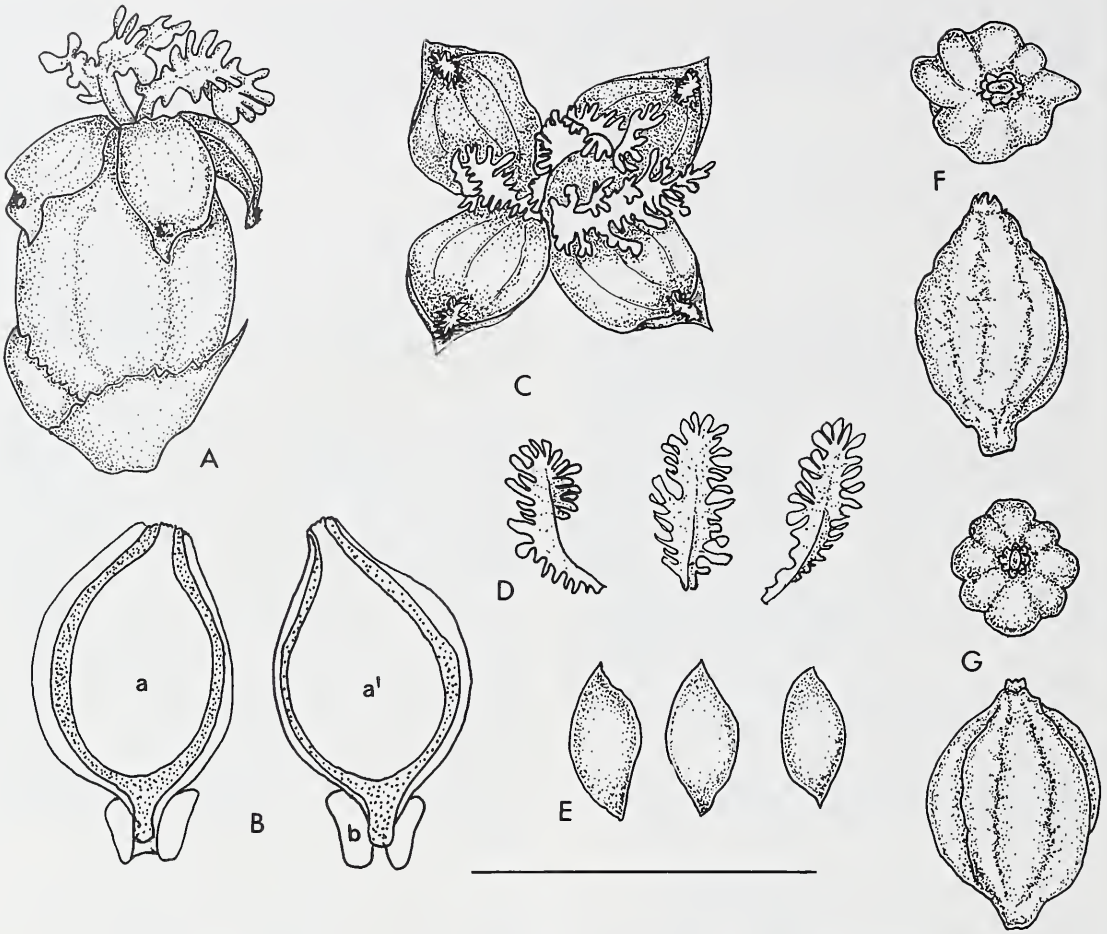


FIGURE 1.—*Cliffortia micrantha*: A, mature fruit with two styles (bracteoles in place, covering the stipe). B, mature fruit in longitudinal section showing flat sides of two achenes (a, a') covered by two layers of tissue; stipe (b) attached; sepals, styles and bracteoles removed. C, top view of three-styled fruit; D, styles from C; E, achenes from C; F, old fruit, side and corresponding top views showing ribs and dorsiventral flattening; G, old fruit, showing four major and four minor ribs in a regular pattern. A–E, *Vlok 2113* (STE); F, *Laidler 154* (STE); G, drawn from *Boshoff 315* (STE). Scale bar = 2 mm.

berg, top of pass into Gamkaskloof, 1 333 m, 8-05-1963, (–BC), *Taylor 4744* (STE); Swartberg, in ravine between Kliphuisvlei and Gamkaskloof, 1 250 m, 7-05-1989, (–BD), *Vlok 2113* (PRE, STE); Noukloof Nature Reserve, gentle SE slope, 566 m, 12-07-1982, (–CA), *Laidler 154* (STE); Roodeberg, S slope near stream, 24-05-1950, (–CB), *Esterhuysen 17152* (NBG).

For number of achenes

CAPE.—3320 (Montagu): Anyserg, S slopes, 810 m, 2-08-1956, (–DA), *Wurts 1424* (NBG); Touwsberg, steep rocky lower S slopes to 1 000 m, 1-06-1956, (–DB), *Esterhuysen 25933* (BOL); Touwsberg, 1 100 m, 11-07-1941, (–DB), *Levyns 7483* (Type) (BOL, NBG, STE). 3321 (Ladismith): Ladismith, koppie 4 miles from town, 566 m, 15-08-1948, (–AD), *Levyns 9030* (BOL); Gamka Mtn Reserve, N slope (moist kloof), 866 m, 03-1976, (–BC), *Boshoff P315* (STE); Prince Albert–Gamkaskloof road, 890 m, 3-08-1979, (–BD), *Bond 1680* (STE); Swartberg, in a ravine between Kliphuisvlei and Gamkaskloof, 1 250 m, 7-05-1989, (–BD), *Vlok 2113* (STE); Noukloof Nat. Res., gentle SE slope, 566 m, 12-07-1982, (–CA), *Laidler 154* (STE); Roodeberg, S slopes near stream, 24-05-1950, (–CB), *Esterhuysen 17152* (BOL, NBG.); Roodeberg, 1 000 m, 10-08-1948, (–CB), *Levyns 8981* (BOL, STE).

Probable hybrid (*C. micrantha* × *C. cervicornu*)

CAPE.—3321 (Ladismith): Swartberg foothills between Bosluis Pass and Die Hel, 10-10-1960, (–BC), *Esterhuysen 28523* (BOL).

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A.C. FELLINGHAM*

* Stellenbosch Herbarium, National Botanical Institute, P.O. Box 471, Stellenbosch 7599.

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ROSACEAE

CLIFFORTIA FASCICULATA, A SUPERFLUOUS NAME FOR *C. AMPLEXISTIPULA*

In his monograph of the genus, Weimarck (1934) placed *Cliffortia amplexistipula* Schltr. under the imperfectly known species. He quoted Schlechter's original description in full (Schlechter 1900) but pointed to the lack of flower and fruit details which did not enable him to identify the species accurately.

This inadequacy led to the description of *C. fasciculata* Weim. (Weimarck 1946). Two years later, Weimarck (1948: 174) stated in one short sentence: '*C. fasciculata* has, however, proved to be identical with *C. amplexistipula* Schltr.' and proceeded to use the latter name in his key.

This fact was also communicated to the Bolus Herbarium as seen in a handwritten note on the sheet of an isotype of *C. fasciculata* Weim. in BOL which reads: 'Weimarck states in a report on material sent, that *C. fasciculata* Weim. is a synonym for *C. amplexistipula* Schltr.' This note is initialed by E. Esterhuysen and dated 10/48.

In Gibbs Russell *et al.* (1987), both *C. fasciculata* Weim. and *C. amplexistipula* Schltr. are listed as correct names.

Weimarck (1934) examined Schlechter's type of *C. amplexistipula*, (Schlechter 8825), from five different herbaria, the one in Berlin presumably being the holotype. As this one was destroyed, I hereby choose the Bolus Herbarium specimen as lectotype of *C. amplexistipula* Schltr.

***Cliffortia amplexistipula* Schltr.** in Botanische Jahrbücher 27: 140 (1900); Weim.: 157 (1934), sub species non sat. cog. Type: In sabulosis prope Ezelbank, in montibus Cederbergen, alt. c. 4000 ped., 2 Sept. 1896, Schlechter 8825 (B⁺, holo.; BOL! lectotype here designated; BM, GRA, K, isolecto.).

C. fasciculata Weim.: 413 (1946). Type: N Cederberg, between Henning (Heuning?) Vlei and Koupoort, 21-10-1945, Esterhuysen 12116 (LD, holo.; BOL!, iso.).

Schlechter's (1900) original description of *C. amplexistipula* (as quoted by Weimarck 1934) did not include flowers and fruit. Weimarck's (1946) description of *C. fasciculata* does include male and female flowers but no fruit.

Description: to augment the description of this species, the following observations are made:

Leaf sheaths: ventral apical portion with persistent red fringe resembling stigma, amplexicaul when young, sometimes splitting when older. **Stipules** minute when young to 0.25 mm long later. **Leaflets:** dorsal surface with raised round spots to the margins ('marginibus subscabridis' of Schlechter), spatulate with mucro minute and ventral in young stage, to elliptic with mucro apical and well developed when mature (Figure 2A & B). **Female sepals:** 3, 1.0–1.2 × 0.6–0.7 mm, fleshy, broadly elliptic, acute, mucronate, glabrous, dorsally with a few small round raised spots (Figure 2C). **Fruit:** (2.6)2.7 × 0.7(0.8) mm,

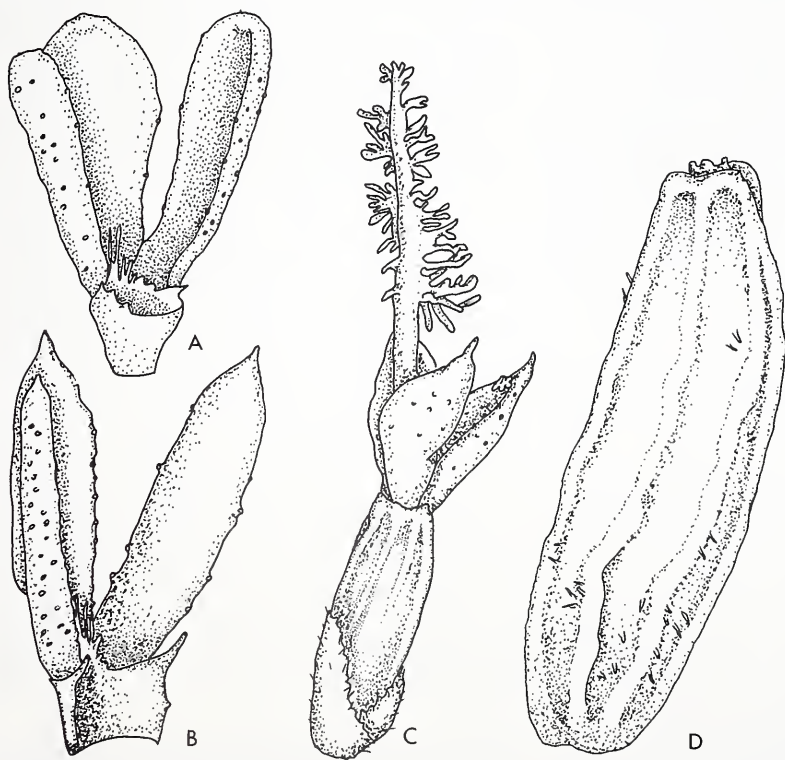


FIGURE 2.—*Cliffortia amplexistipula*, Oliver 10046 (STE): A, adaxial view of young leaf, short shoot bearing young fruit (C) removed; B, adaxial view of older leaf, sheath opened; C, young fruit with calyx, stigma and bracts still attached; D, mature fruit. Scale bars = 1 mm.

narrowly oblong, slightly curved, 7(8)-ribbed with two ribs flattened and extended around base forming continuous narrow wing, surface minutely scabrid to papillate in places (Figure 2D).

Distribution and habitat: *C. amplexistipula* occurs on the drier inland mountains, from the Kamiesberg in the north to the Anysberg in the Little Karoo, in arid fynbos on sandstones and quartzites, often on southern slopes or in the lee of a rock.

Specimens examined in addition to the types

CAPE.—3018 (Kamiesberg): Namaqualand, Welkom, Khamiesberg near Garies, 1 100 m, 16-10-1954, (—AC), *Esterhuysen 23711* (BOL). 3118 (Vanrhynsdorp): Gifberg, 480 m, 14-07-1974, (—DC), *Thompson 2088* (STE). 3119 (Calvinia): Calvinia Lokenburg, arid fynbos of TMS ridges, 770 m, 28-08-1958, (—CA), *Acocks 19719* (BOL); Lokenburg, on rugged sandstone hills, 31-05-1964, (—CA), *Esterhuysen 30707* (BOL). 3218 (Clanwilliam): South Cold Bokkeveld, Ceres, 4-10-1940, (—AB), *Bond 662* (NBG); Baviaansberg, Ceres, 1 450 m, 2-01-1942, (—BA), *Compton 12877* (NBG). 3219 (Wuppertal): Cederberg, Heuning Vlei, 29-12-1941, (—AA), *Esterhuysen 7468* (BOL); Clanwilliam Div., Cederberg, Tafelberg, shale band, 25-09-1942, (—AC), *Esterhuysen 8092* (BOL); Clanwilliam Div., foot of Tafelberg, shale band, 1 500 m, 29-12-1947, (—AC), *Esterhuysen 14326* (BOL); Clanwilliam Div., Duivelsgat, S Cederberg (Sneeuwberg area), 11-10-1946, (—CA), *Esterhuysen 13101* (BOL); Ceres Div., Zuurvlakte, E of Bokkeveld Sneeuwkop area, 20-04-1946, (—CD), *Esterhuysen 12744* (BOL, NBG, SAM); Ceres, Stompiesfontein, Swarttruggens, streambanks, 1-11-1961,

(—DC), *Esterhuysen 29305* (BOL); Ceres, Stompiesfontein, Swarttruggens, rocky plateau, 1 100 m, 1-11-1961, (—DC), *Esterhuysen 29327* (BOL). 3319 (Worcester): Gydo, Ceres, 1 000 m, 10-11-1946, (—AB), *Compton 18752* (NBG); Cold Bokkeveld, Winkelhaak area, flats NW of Jakkalsdam, 960 m, 13-02-1992, (—AB), *Oliver 10046* (STE). 3320 (Montagu): Laingsburg, Witteberg, on stony rocky south slopes, 1 300 m, 31-01-1961, (—AD), *Esterhuysen 28867* (BOL, NBG); kloof on S slopes of Anysberg, Little Karoo, 22-05-1950, (—DA), *Esterhuysen 17077* (BOL); Anysberg, summit plateau, in lee of rock, 10-08-1991, (—DA), *Fellingham 1537* (STE).

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A.C. FELLINGHAM*

* Stellenbosch Herbarium, National Botanical Institute, P.O. Box 471, Stellenbosch 7599.

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FABACEAE

VIGNA KOKII, A NEW SPECIES FROM SOUTHERN AFRICA

Vigna kokii B.J. Pienaar, sp. nov. (Sect. *Microspermae*—Papilionoideae), *V. mudeniae* B.J. Pienaar facie caulibus pedunculis distincte costatis alatis similis; *V. richardsiae* Verdc. (Sect. *Microspermae*) stipulis reflexis auriculis lateraliter libris caule connatis similis; a *V. monophylla* Taub. (Sect. *Haydoniae*) glandibus basalibus verticillo interiore antherarum absentis differt; styli extensio 'tumore' in textura reducta ubi versus stigma laterale flexa (non ut in *V. mudenia* extensione 'digito primo' et in *V. monophylla* tota absentia); reticulum extinae granorum pollinis vix manifestum.

TYPE.—Transvaal, 2530 (Lydenburg): Schagen, woodland 0.8 km from Crocodile Hotel on road to Rosehaugh, *Pienaar 1364* (PRE, holo.; K, P, iso.).

Rootstock carrot-shaped, at length woody. **Stem** erect in youth, twining at length, somewhat ridged to alate, scarcely strigose to patent with light hairs. **Leaflets** oblong with apex and base rounded in juvenile stage, $\pm 25\text{--}58 \times 0.8\text{--}30.0$ mm, surface smooth to touch, adnately strigose, thickest along dorsal nerves and lamina margin, rhomboid to sublobular with rounded lobes at maturity, $\pm 80 \times 60\text{--}70$ mm at broadest point, apices abruptly narrowed, obtuse, apiculate, base cuneate to obtuse, papyraceous, strigose. **Stipules** with cordate base, laterally auriculate at maturity, lanceolate, reflexed, $\pm 6.0 \times 1.5$ mm, acuminate, margins ciliate; in youth base more or less elongated, truncate (cf. *V. mudenia* B.J. Pienaar 1991).

Inflorescence contracted, peduncles alate, bearing at apex one pair of yellowish green flowers, flushed violet, with vertical row of extrafloral nectary glands between them (Figure 3B). **Calyx** campanulate, lobes, ± 2 mm, acute with broad bases, \pm as long as tube or shorter, tube up to 3.25 mm long, upper pair of lobes connate for $\frac{1}{3}$ to $\frac{1}{2}$ their length, strigose. **Standard** ovate to oblate, emarginate, $\pm 10\text{--}14$ mm long, spur straight with inferior callosities divergent, auricular, superior callosities divergent, narrow (vestigial). **Wings** narrowly ovate, $\pm 10.0 \times 5.5$ mm, auricle slender with raised cell sculpturing (almost papillate). **Keel** ± 11 mm long, obtuse, slightly upturned. **Filament tube** ± 10 mm long, free filaments in two whorls, 3 or 4 mm long, anterior filament geniculate at base, ± 13 mm long; anthers oblate, glands at base absent. **Ovary** pubescent, $\pm 9\text{--}10$ mm long, style broadened and flattened as it curves upward, pollen brush on anterior face, apically twisted at maturity, accentuated protuberance of style prolongation absent but stylar tissue swollen as it bends toward stigmatic papillae at somewhat more than 90° . **Pollen** grains scarcely reticulate, muri low, rounded. **Legumes** beaked, ± 68 mm long, scabrid with long, stiff hairs along margin, 18-seeded. **Seeds** 3.4 mm long, yellowish brown to dark brown, black mottled around hilum, hilum scarcely eccentric, aril scarcely developed or absent. Figure 4.

NAMIBIA.—1724 (Katima Mulilo): 20 km SW of Katima Mulilo, (—CA), *De Winter 9180* (PRE). 1821 (Andara): Caprivi side of river, near Andara Mission Station, (—AB), *De Winter & Marais 4812* (PRE); Dico, Andara, (—AB), *Giess 15572* (WIND).

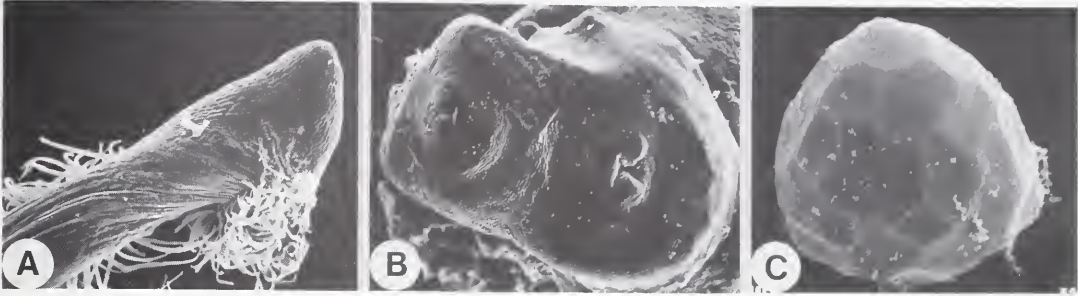


FIGURE 3.—*Vigna kokii*, Pienaar 1364 (PRE): A, style prolongation, reduced to a swelling, $\times 33$; B, extrafloral nectaries, $\times 30$; C, pollen grain, $\times 458$.

TRANSSVAAL.—2431 (Acornhoek): Nwanetzi, Kruger National Park, (—AD), Coetzee 6062 (PRE). 2527 (Rustenburg): mountainside, Saulspoort, (—AA), Germishuizen 514 (PRE). 2530 (Lydenburg): Schagen, Farm of J.J. van Niekerk, Nelspruit District, (—BD), Liebenberg 3297 (PRE); 0.8 km from Crocodile Hotel on turnoff to Rosehaugh, (—BD), Kok & Pienaar 1297 (PRE, PRU), Pienaar 1364 (PRE).

Found in dense undergrowth of dry woodland in the Transvaal and in Caprivi in northeastern Namibia. Figure 5.

In general facies *V. kokii* is very similar to *V. mudenia* B.J. Pienaar (1991), with the stems and peduncles distinctly alate and the contracted inflorescence bearing two yellow-green flowers, but the leaflets are oblong with rounded base and apex in youth, becoming rhombic or sublobular at maturity. *V. kokii* is similar to *V. richardsiae* Verdc. (Sect. *Microspermae*) in having stipules reflexed, connate with the stem but with auricles laterally free; it differs from *V. monophylla* Taub. (Sect. *Haydonia*) in the absence of basal glands on the interior whorl of anthers; the style

prolongation (Figure 3A) is reduced to a 'swelling' in the tissue of the style where it bends toward the lateral stigma, as opposed to the 'finger tip' protuberance of *V. mudenia* and total absence of any prolongation in *V. monophylla*; the exine sculpture of the pollen grains (Figure 3C), appears more rounded than that of *V. mudenia* as opposed to the total loss thereof in *V. monophylla*. These characters support the decision to keep it in the same section as *V. mudenia* but to accept it as a new species. Its distribution also differs from that of *V. mudenia*.

The styler thickening (rather than a true protuberance), at the bend toward the lateral stigma, may represent an evolutionary stage more advanced than in other members of the section *Microspermae*. This trend probably reflects an incipient stage toward the loss of the styler beak, as displayed in the subgenus *Haydonia* (Pienaar 1992). The reticulation of the pollen grains has almost disappeared, a further development toward the eventual smoothness of the exine in section *Haydonia* (e.g. *V. monophylla* Taub.).

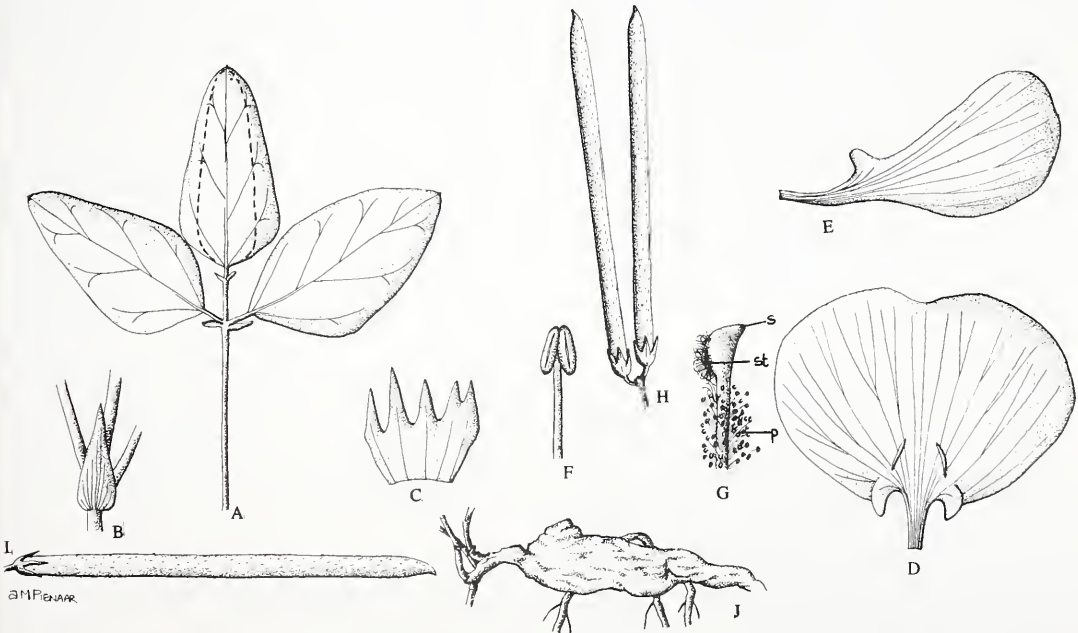


FIGURE 4.—*Vigna kokii*, Pienaar 1344 (PRE): A, leaf, $\times 1$; B, stipule, $\times 3$; C, calyx, $\times 3$; D, standard with two pairs callosities, $\times 4$; E, wing, $\times 4$; F, anther, $\times 7$; G, style prolongation (s), stigma (st), pollen brush with pollen (p), $\times 10$; H, legumes on peduncle, $\times 1$; I, legumes, $\times 1$; J, underground tuber, vertical, $\times 0.25$.

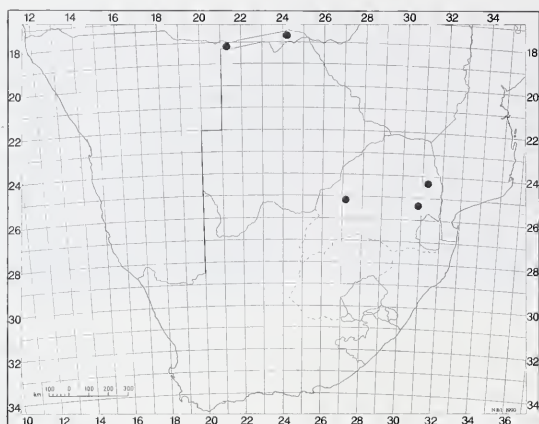


FIGURE 5.—Known distribution of *Vigna kokii* in southern Africa.

It gives me great pleasure to name this new species after Prof. P.D.F. Kok, under whose guidance my taxonomic work on the genus *Vigna* was initiated. One of the first collections (in 1934) of the new species is *Liebenberg 3297* (PRE), from a farm in the Schagen District. Prof. Kok

accompanied me on the first field trip to the Schagen area in search of more material of the new species. He searched as hard as I did until an immature plant was found in the thickets and I was able to return to the locality a season later. He also financed the trip.

ACKNOWLEDGEMENTS

I wish to thank Prof. A.E. van Wyk for his academic assistance, the University of Pretoria and the National Botanical Institute for putting their amenities at my disposal, Mrs S. Perold for the SEM micrographs and Mrs A. Romanowski for her photographic skills, Dr D.J.B. Killick for the Latin diagnosis and Miss A. Pienaar for the line drawings.

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B.J. PIENAAR*

* Present address: P.O. Box 44057, Linden, Johannesburg 2104.
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ASTERACEAE

AN EVALUATION OF HUTCHINSON'S 'BEETLE-DAISY' HYPOTHESIS

INTRODUCTION

Some Cape Asteraceae species have conspicuous dark markings on their ray florets. Such markings are usually interpreted as 'guides' of various sorts (e.g. Faegri & Van der Pijl 1979). However, Hutchinson (1946) suggested that the dark raised marks on the ray florets of *Gorteria diffusa* Thunb. mimicked herbivorous beetles burrowing head down in the inflorescences. He noted that this species appeared to have few beetle visitors and to suffer less herbivory than other Asteraceae (such as an *Arctotis* sp.) growing nearby. He hypothesised that the marks repelled the beetles. In his review of plant mimicry worldwide, Wiens (1978) considered this an exceptionally intriguing example of Batesian mimicry. Despite this there still appears to be a dearth of information on the interaction between beetle-daisies and beetles. The purpose of this note is to extend the concept of beetle-daisies and to test Hutchinson's hypothesis.

The beetles which commonly burrow into daisy flowers are known as monkey-beetles (Coleoptera: Scarabaeidae: Rutelinae/Hopliinae; Scholtz & Holm 1985). The subfamily to which they belong is largely centred in the Cape. Little is known about their ecology against which to test Hutchinson's hypothesis. The situation regarding the relative absence of monkey-beetles on *Gorteria diffusa* observed 45 years ago by Hutchinson remains unchanged today (pers. obs. in Nieuwoudtville District). I did not see any hopliinid visitors on this species in many hours of observation in the spring of 1990. Since the hopliinids are a large group and they visit many other plant species (Whitehead, Giliomee & Rebelo 1987; pers. obs.), Hutchinson's hypothesis may be of more general relevance.

Assuming this, I studied the interaction of *Arctotheca calendula* L. (Cape weed), a weedy daisy without dark markings on the ray florets, and the beetle *Heterochelus sexlineatus* Thunb., a herbivorous species with strong cutting mandibles. This plant species is visited by many hopliinid species (Scott & Way 1990) and I observed *Heterochelus sexlineatus* visiting at least seven other plant species at the study site, suggesting that there is only a diffuse relationship between the two study taxa.

In *Gorteria diffusa*, the so-called beetle-daisy, the 'beetle' mark is a dark raised bump on the ray floret with a white spot in the middle and with yellow 'legs'. Under ultraviolet light this 'beetle' does not appear significantly different (pers. obs.). The number of 'beetles' per inflorescence is very variable (from none to a full ring with marks on all ray florets) within and between individuals (pers. obs.). The 'beetles' on inflorescences with a full ring appear to be the least derived condition because they are poorly differentiated and are similar in appearance to many other Asteraceae with a ring of conspicuous dark basal markings on ray florets (e.g. *Gazania lichtensteinii*). Even *Arctotis* species (e.g. *A. gumbletonii* Hook. f.), which Hutchinson (1946) suggested suffer more predation, have complex dark basal markings on the ray florets.

It is thus possible that any dark marks near the base of the ray floret or darkening of the disc found in other genera such as *Osteospermum*, *Dimorphotheca* and *Ursinia* may be mimicking beetles. In the Still Bay area, J. Vlok and I noted an *Ursinia* species (close to *U. paleacea* (L.) Moench) which also appears to be a beetle-daisy. In this

TABLE 1.—Number of *Heterochelus sexlineatus* beetles on manipulated and unmanipulated inflorescences of *Arctotheca calendula*. For plots 1 and 2 extra beetles were released (see text)

Treatment	Plot 1		Plot 2		Plot 3	
	Sample size	No. (%) with beetles	Sample size	No. (%) with beetles	Sample size	No. (%) with beetles
Control	150	26 (17)	50	11 (22)	250	15 (6)
Black dots	73	15 (21)	24	5 (21)	50	4 (8)
Removed petal	73	10 (14)	23	7 (30)		
Yellow dots					50	2 (4)
Brown dots					50	3 (6)

species some of the ray florets have been lost and through the gaps they have left, large dark involucre bracts appear. This exceptional modification is equally impressive in the field as that of *Gorteria diffusa*. *Ursinia* is placed in the tribe Anthemideae whereas all the other genera mentioned are in the Arctotideae, indicating strong floral convergence. According to K. Bremer (pers. com.) these types of dark markings are probably restricted to the Cape Asteraceae. If all the above modifications are shown to be a response to monkey-beetles then I estimate that about 30 Cape species could display the ‘beetle-daisy’ syndrome (see Midgley 1991 for photographs of most of above examples).

The following information was collected to test Hutchinson’s hypothesis; (i) do numbers of beetle visitors differ between inflorescences with artificial beetle marks and those without, (ii) do numbers of beetles on unmanipulated inflorescences suggest that the presence of one beetle deters others?

MATERIAL AND METHODS

The behaviour of the hopliinid *Heterochelus sexlineatus* was observed on a large (> 500 individuals) population of *Arctotheca calendula* growing wild in an arboretum at Saasveld, near George in the southern Cape.

Sampling took place on warm days between 15h00 and 16h00 during October 1990. Inflorescences were manipulated by marking the ray florets with brown, yellow and black dots using commercial Artline pens. The yellow marks were not visible (to human eyes) on the yellow ray florets and thus served as controls to determine any other non-visual effects of the marks on beetles. Numbers of dots ranged from two to five and were approximately the same size as the beetle. To simulate the *Ursinia* type model (described above), from three to five ray florets were removed from a sample of inflorescences. Inflorescences were checked the following day for numbers of beetles. In some cases inflorescences became unsuitable subsequent to marking and this accounts for unequal numbers on Table 1. Because the numbers of beetles per inflorescence are low (less than 5% —see Results and conclusions) in some instances beetles were captured from other areas and released in the vicinity of study plots.

RESULTS AND CONCLUSIONS

Surveys indicated that 10 out of 200, six out of 100 and nine out of 300 *Arctotheca* inflorescences had beetle visitors (mean of less than 5% of inflorescences had visitors). *Ursinia anthemoides* (L.) Poir. in the vicinity had less than

2% of inflorescences with visitors. The manipulation experiments indicate that this beetle is virtually indifferent to markings on the ray florets and to the absence of ray florets (Table 1). The fact that considerable aggregation of beetles occurs on inflorescences (e.g. up to eight individuals in Table 2) suggests that the presence of an individual is not inimical to others. Approximately twice as many male beetles as females were found (Table 2). Relative to the number of inflorescences, the beetles, and especially the females, are rare. Consequently males probably visit many inflorescences searching for mates. The males fight for access to females (Midgley 1992). This suggests that this beetle would be an effective pollinator (its hairy body is often covered with pollen) but a relatively insignificant herbivore (a few florets in a few inflorescences in a population are damaged). The results concerning manipulated inflorescences suggest that floral markings have no negative effect on visitation. It is possible that beetles are actually attracted to the marked florets. However, on discovering that there are no real beetles on the florets, they fly off. It was not, however, possible to observe each visitor as it arrived on all manipulated inflorescences simultaneously to see whether this was the case. Although the hopliinid considered in this study is a herbivore with strong cutting mandibles, many other hopliinids are merely pollen feeders (Peringuey 1902). It would make little sense for mimicry to evolve to repel the non-herbivorous, pollen-carrying hopliinid beetles. Also there would be little reason for an evolutionary trend towards reduction in the number of beetle marks, if their function is repulsion.

TABLE 2.—Distribution by gender of *Heterochelus sexlineatus* beetles (M = male, F = female) in three samples of inflorescences of which each had at least one beetle visitor

	Samples		
	1	2	3
1M	27	35	31
1F	1	3	4
1M1F	12	8	7
2F	0	0	2
2M	1	2	0
2M1F	7	4	9
2M2F	5	4	2
1M1F	3	3	1
3M1F	1	0	3
2M3F	1	1	0
3M3F	0	0	1
4M3F	1	0	0
4M4F	1	1	0
4M1F	0	1	0
TOTAL	60	60	60

The above (no repulsion, aggregation and feeding habits) suggest that Hutchinson's hypothesis is not complete. If the markings act as mimics then it is probably to attract beetles, presumably for their role in pollination. This would then be a case of reproductive mimicry (sensu Wiens 1978), similar in a way to pseudocopulatory orchids. Obviously this study of one beetle and daisy species needs to be broadened before Hutchinson's intriguing hypothesis of this little-studied syndrome of Cape plants is fully tested.

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J.J. MIDGLEY*

* CSIR, Division of Forest Science and Technology, Private Bag X5011, Stellenbosch 7599.
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OXALIDACEAE

A NEW SPECIES OF *OXALIS* FROM THE WESTERN CAPE

Oxalis oculifera E.G.H. Oliver, sp. nov. in Sectione *Latifoliolatis*, in genere singularis propter tubum corollae rubrum papillatum partem alterum violaceo-roseum annulo mediano alba, foliola subpeltata subparallela glauca.

Planta parva, 5–15 mm alta. *Bulbus* ovoideus, 8 × 6 mm, ferrugineus, vaginis papyraceis tectus, vaginis in parte inferiore diagonaliter secedentibus. *Folia* 1–9; petiolus 2–20 mm longus, sparse glandulopilosus, roseus; foliola 3, interdum 2 vel 1, subparallela, 3.0–4.5 × 3.0 mm, semiconduplicata, oblique subpeltata, basaliter subinfundibuliformia, late elliptica ad obovata, interdum oblongo-elliptica, apice late obtusa vel plus minusve emarginata base obtusa, glauca, adaxiale dense papillata, abaxiale glabra sed interdum locis parvis croceis callosis, margine hyalino et intra zona crocea gracili callosa; petioli 0.3–0.6 mm longi. *Pedunculi* uniflori, 20–37 mm longi, erecti demum prostrati, sparse glandulopilosos, rosei; bractae absentes interdum 1 vel 2 in parte superiore, filiformes vel lineares, ad 0.6 mm longae, sparse glandulopilosae. *Sepala* 1.7–1.9 × 0.7–0.9 mm, appressa, ovata ad late ovata, interioria angustissima, subacuta, rasilia et sparse glandulopilosa, zona marginali atropurpurea et zona proximae interiore aurantiaca callosa, parte cetera viridi erubescens. *Corolla* ± 9–10 mm longa, late saliformis, violaceo-rosea fauce cum annulo albo et tubo vinaceo-rubro; petala 5–6 mm lata, oblique obovata ad late subspathulata, base parum conjuncta, abaxiale sparsissime glandulopilosa, ecallosa, adaxiale in zona rubra papillata. *Stamina* in seriebus tribus, base longitudine 0.5–0.8 mm conjuncta; antherae albae marginibus atropurpureis; filamenta purpurea sparse glandulopilosa; pollen tricolporatum, ellipsoideum, in antheris superioribus medianisque album, in antheris inferioribus luteum. *Ovarium* 0.7–1.0 mm longum, ovoideum, uniovulatum, in parte superiore sparse glandulopilosum; styli in seriebus tribus,

mediani superioresque erecti ad parum patentes, inferiores valde porrecti, sparse glandulopilosos purpurei; stigmata fimbriata, superiora medianaque purpurea, inferiora alba. Figura 6.

TYPE.—3118 (Vanhynsdorp): Cape Province, Vanhynsdorp Dist., Gifberg/Matsikamma area, central plateau W of van Taakskom near top of the pass, 595 m, (–DD), 12-06-1990, *Oliver 9558* (STE, holotype; BOL, K, PRE isotypes).

Dwarf stemless plants 5–15 mm high, aggregated into clumps. *Bulb* ovoid, 8 × 6 mm, light reddish brown, covered with papery sheaths splitting diagonally in lower part. *Rhizome* vertical up to 20 mm long. *Stem* none or very short up to 4 mm long. *Leaves* 1–9 per plant; petiole 2–20 mm long, sparsely glandular pilose, pinkish; leaflets mostly 3, occasionally 2 or 1, subparallel, 3.0–4.5 × 3.0 mm, semiconduplicate, obliquely subpeltate, basally subinfundibuliform, broadly elliptic to obovate, occasionally oblong-elliptic, apically broadly rounded or slightly emarginate basally rounded, glaucous, adaxially densely papillate, abaxially glabrous, with hyaline margin and inside this a thin orange callose zone, sometimes with scattered small orange callose patches abaxially; petiole 0.3–0.6 mm long. *Peduncle* 1-flowered, 20–37 mm long, erect becoming prostrate, markedly glandular pilose when young and short, becoming sparsely so when mature, pinkish; bracts usually absent, sometimes 1 or 2 on upper part of peduncle, filiform or linear up to 0.6 mm long, sparsely glandular pilose. *Sepals* 1.7–1.9 × 0.7–0.9 mm, adpressed to corolla and joined at base, lobes ovate to broadly ovate with inner ones narrowest, subacute, glabrous and sparsely glandular pilose, with very dark purple marginal zone and orange callose zone just inside that, the rest green becoming reddish. *Corolla* about 9–10 mm long, broadly salver-shaped, violet-pink with white

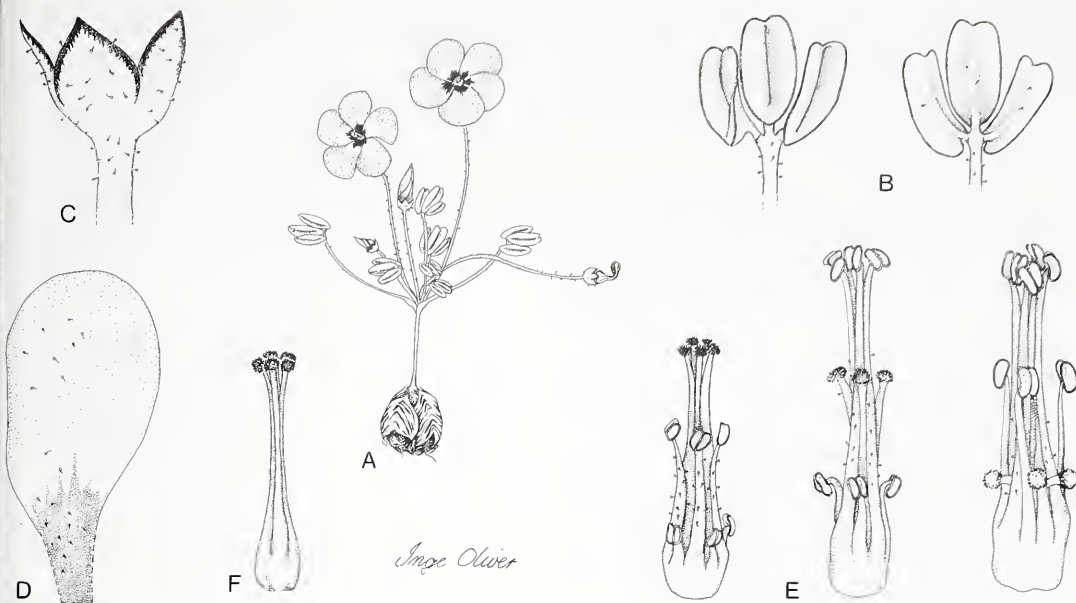


FIGURE 6.—*Oxalis oculifera*: A, plant, $\times 2$; B, leaf, adaxial view, on left, & abaxial view, on right, $\times 12$; C, calyx, $\times 25$; D, petal, abaxial view, $\times 25$; E, the three trimorphic series of the androecium and gynoecium, $\times 25$; F, gynoecium, $\times 25$. All drawn from the type, *Oliver 9558* (STE).

ring in throat and wine-red tube; petals 5–6 mm wide, obliquely obovate to broadly subspathulate, joined slightly at base, very sparsely glandular pilose abaxially on outer margin, ecallose, papillate adaxially on red zone. *Stamens* in 3 series, 2 series per plant, the shortest 1.2 mm long, the middle 2.0–2.3 mm long, the longest 3.0–3.5 mm long, all joined for 0.5–0.8 mm at base, the uppermost manifest, the rest included; anthers white with dark purple edges; filaments purplish, sparsely glandular pilose; pollen tricolporate, ellipsoid, in upper and middle anthers white, in bottom anthers yellow. *Ovary* 0.7–1.0 mm long, ovoid, sparsely glandular pilose in upper half, 1-ovuled; styles in 3 series, the lowest 0.5 mm long, markedly spreading and white, the middle 1.2 mm long and the uppermost series 3 mm long, the latter two series erect to slightly spreading purplish sparsely glandular pilose; stigmas fimbriate, the uppermost and middle series purple, the lower series white. Figure 6.

This new species of *Oxalis* is remarkable in the genus on account of the colour of its corolla and the distinctive shape of its leaves. The corolla tube is wine-red with a white ring in the throat, the rest of the corolla being violet-pink. The glaucous leaflets are unusual for being obliquely peltate with the petiolule attached abaxially to the lamina. The leaflets are subparallel next to each other and not spreading. They are semiconduplicate in a broad V-shape with the basal portion above the petiole often partially funnel-shaped.

O. oculifera falls within the Section *Latifoliolatae* which Salter (1944) described as an unnatural assemblage of species. It is defined as having those species forming acaulescent plants with broad, but never linear or oblong, leaves. Within the section this species is probably most closely allied to *O. petiolulata* Bol. f.

O. petiolulata appears to be confined to the central and northern parts of the Cedarberg near Clanwilliam where it is known from only three collections, all in BOL (*H. Bolus* 8952, the type; *Adamson* in BOL 20492 and *Pocock s.n.*). All three have very differently sized leaves with *Adamson* in BOL 20492 having the smallest leaves most similar to those in the new species. The Pocock specimen has no flowers and was determined with a query by Salter.

In *O. petiolulata* the plants are very sparsely and minutely glandular pilose, not glabrous as recorded by Salter. The sepals are sparsely ciliate with short rather thick hairs. The leaflets have about six distinct black callose 'lumps' towards the edges and nothing submarginally, whereas in the new species the callose dots are small, orange in colour and are randomly scattered and there is a distinct, very thin, submarginal orange callose line. In *O. petiolulata* the callose region on the sepals is black and confined to two large patches near the apex, whereas in the new species the callose region is orange and submarginal down the sepal just below the thin marginal black zone.

The bulbs in *O. oculifera* are quite different from those in *O. petiolulata*. In the former the bulb is small and ovoid, the tunics splitting with diagonal slits like an inverted V, whereas in the latter they are narrowly ovoid and attenuate with longitudinally splitting tunics.

The leaflets in the new species are very distinctive. They are subparallel, adpressed and partially conduplicate. The glaucous-grey colour of the leaves is very striking in the living material. This is produced by numerous translucent, shortly papillate cells on the upper surface. The remarkable feature is the position of the point of attachment of the leaflet to the petiolule. In *O. petiolulata* the petiolule

is attached at the base of the lamina. In *O. oculifera* the petiole is attached about one quarter of the way along the undersurface of the lamina which is thus semipetate. In some leaflets the two sides of the basal portion of the lamina are a little more adnate producing a slightly funnel-shaped base to the leaflet.

Salter (1944) noted that he had not seen any living material of *O. petiolulata* but described the flowers as 'deep pink with a purple eye in the throat, tube dull yellow'. F. Bolus (1918) described the corolla from his father's collection as 'purpurea' and Adamson gave 'deep pink with a dark throat' on his label. This would indicate that the corolla was tricoloured with a purple ring at the mouth of the tube which is yellow, quite unlike the very distinctive wine-red tube forming the eye in *O. oculifera*. Salter (1935) when describing his *O. oculata* (= *O. callosa* R. Knuth) gave the colours as 'roseo-rubra...tubo luteo, in faucibus purpureo-annulata' and noted that the dark purple 'eye' in the corolla mouth is a character which he found in some forms of other species, but in *O. callosa* it appeared to be always present. His drawing which was repeated under *O. callosa* (Salter 1944), shows the dark 'eye' as a ring in the mouth of the corolla.

This feature of the red tube was mentioned to Salter when I made the first collection in 1965. I told him I had noted that all the flowers in the population possessed the striking red eye. He remarked that this was unknown to him in the genus and that the material constituted a distinct new species.

O. oculifera is confined to one major population and several nearby smaller populations in a small area on the summit of the mountain plateau between the Gifberg and Matsikamma Mountains (Figure 7). I have not been able to locate any other populations, which could very well be found on this extensive range with more intensive searching. The plants occur in shallow gritty sand on quartzitic sheet rock of the Table Mountain Group. The main population grows where water seeps over the rock, in some places as a small streamlet, the plants standing in the shallow water. The plants are dominant, forming pure stands of many individuals or clumps which are a remarkable sight when in full bloom in May and early June, a month after the first autumn rains.

This contrasts with the spring flowering period, September/October, for *O. petiolulata* for the Bolus and Pocock collections. Surprisingly the Adamson collection was collected in flower in May 1933. Pocock recorded her collection as 'growing in marshy places and slowly flowing streams'.

Salter (1944) noted that all the native South African species are trimorphic. He mentioned that overseas workers had recorded that the pollen in *Oxalis* was of different sizes. Salter himself had noted that the colour of the pollen varied but that he had not recorded the details for the South African species. *O. oculifera* is trimorphic within the populations studied and possesses two distinct pollen types (Figure 6E). White larger grains are produced by the middle and uppermost anthers and yellow smaller grains by the lowest set of anthers. This feature raises the intriguing problem of pollen selection in the pollination

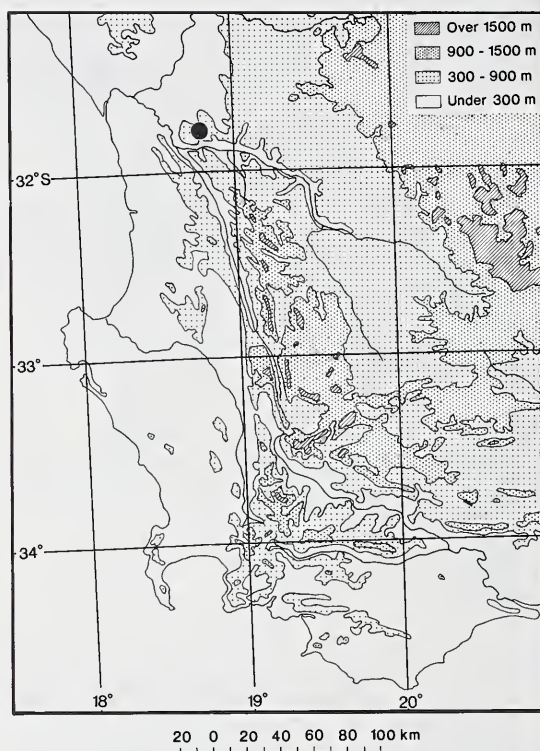


FIGURE 7.—The known distribution of *Oxalis oculifera*.

syndrome of the species. In the wild no insect visitors other than the occasional thrips crawling around in the flower, were observed.

The material studied for this species included living material of *Oliver* 9558 flowering in cultivation at Stellenbosch during May 1992.

Specimens examined

O. oculifera

CAPE.—3118 (Vanhynsdorp): Vanhynsdorp Dist., Gifberg/Matsikamma area, central plateau W of Van Taakskom near summit of the pass, 595 m, (—DD), 10-06-1965, *Oliver* in STE 32028 (PRE, STE, MO); *ibid.*, 12-06-1990, *Oliver* 9558 (BOL, K, PRE, STE).

O. petiolulata

CAPE.—3219 (Wuppertal): Clanwilliam, Cedarberg, Krakadouw, 1 000 m, (—AA), 3-05-1933, *Adamson* in BOL 20492 (BOL); near Wuppertal and Krakadouw, 1 000 m, (—AA/AC), 8-10-1897, *H. Bolus* 8952 (BOL, holo.); Cedarberg, between Middelberg hut and Crystal Pool, 1 220–1 525 m, (—AC), 09-1930, *Pocock* s.n. (BOL).

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E.G.H. OLIVER*

* Stellenbosch Herbarium, P.O. Box 471, Stellenbosch 7599.
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PTERIDOPHYTA—ADIANTACEAE

A NEW CYTOTYPE FOR *ACROSTICHUM AUREUM*

Acrostichum is a genus with a pantropical distribution and consists of three, or perhaps more, species. *A. aureum* L. is the most widespread of these and also has a pantropical distribution.

On the west coast of Africa *A. aureum* occurs from Guinea-Bissau to northern Angola and on the east coast from Zanzibar to the Transkei. *A. aureum* is largely an estuarine species which is commonly associated with the upper edge of mangrove communities. It generally grows in brackish or saline flats of alluvial mud or muddy sands. Although it is predominantly an estuarine species it occurs sporadically at considerable distances from the coast. In Zimbabwe it was found at an elevation of approximately 500 m at a hot spring with salt efflorescences (Jacobsen 1983). Plants have also been recorded 100 km from the coast in Saudi Arabia, 823 m above sea level, where it grows in a slightly saline alkaline seepage (Collenette 1991).

Cytological observations in *A. aureum* have been carried out on plants from Sri Lanka (Manton & Sledge 1954), Ghana (Manton 1959), southern India (Abraham *et al.* 1962) and Jamaica (Walker 1966). In all events the chromosome number reported was $2n = 60$.

A collection of *A. aureum* made by me, Roux 1945 (NBG), in a seasonally marshy area on the banks of the St Lucia Estuary, on the northern Natal coast, have now been studied cytologically. Acetocarmine preparations of root tips taken from this cultivated plant revealed a chromosome number of $2n = 120$ (Figure 8). This plant may therefore be considered a tetraploid. The suggestion made by Tryon & Tryon (1982) that polyploidy, which is a common phenomenon in tropical pteridophytes, never developed in the genus, can therefore no longer be upheld. Most chromosomes are of the acrocentric and telocentric type with few being submetacentric.



FIGURE 8.—Root tip mitosis of *Acrostichum aureum* showing 120 chromosomes, Roux 1945 (NBG).

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J.P. ROUX*

* Compton Herbarium, National Botanical Institute, Private Bag X7, Claremont 7735.
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FIGURE 9.—*Argyrolobium rotundifolium*, Edwards & Ackermann 329 (NU). A, habit; B, leaf; C, fruit; D, standard, frontal view; E, keel; F, wing; G, calyx; H, androecium. Scale bars: A = 10 mm; B = 5 mm; C = 4 mm; D–F, H = 2 mm; G = 4 mm.

FABACEAE

NOTES ON THE GENUS *ARGYROLOBIUM* (CROTALARIEAE) INCLUDING A NEW SPECIES FROM SOUTHERN AFRICA

Argyrobium rupestre (E. Mey.) Walp. comprises 'small slender-stemmed few-flowered prostrate or shortly ascending plants from mountainous areas the length of eastern Africa' (Polhill 1968). Tropical representatives of *A. rupestre* have been 'loosely subdivided' into four subspecies by Polhill (*l.c.*). The complex is notoriously difficult to classify due to the poor resolution of characters and Polhill (*l.c.*) concedes that 'some of the forms may possibly have evolved separately from more robust local species but whatever their origin only slight differences in habit and indumentum distinguish them'. Whereas his revision covered high altitude specimens from South Africa, no mention was made of the lowland element discussed here and routinely included within *A. rupestre*.

***Argyrobium rotundifolium* T. J. Edwards, sp. nov.**, *A. rupestri* affinis sed habitu prostrato; foliis suborbiculatis cum pilis rufo-tomentosis; corolla alis sine sculptura differt.

TYPE.—Natal, 2930 (Pietermaritzburg): between Peacevale & Drummond, (—DD), *Edwards & Ackermann 329* (NU, holo.; K, E, PRE, iso.).

Herbaceous perennial, up to 150 mm tall, but usually prostrate, well branched, stems shortly rufous-tomentose, becoming glabrous. *Leaves* moderately tomentose above, densely tomentose beneath; leaflets broadly ovate to suborbicular 14–32 × 10–25 mm, petiole tomentose, 10–30 mm long; apex obtuse to rounded, apiculate; margins densely rufous-tomentose; stipules free, setaceous to lanceolate, up to 10 × 1.5 mm. *Inflorescence* pseudumbellate, 1–4(–6)-flowered, initially terminal but becoming leaf-opposed; peduncle (30–)40–150 mm long; bracts linear or narrowly elliptic, up to 6 × 1 mm, bracteoles linear, up to 3 mm long. *Flowers* dimorphic. *Calyx* sparsely to densely pilose; upper lobes 8–10 mm long, lower lip 8–10 mm long, lobes 3–4 mm long. *Corolla* bright yellow becoming russet; standard suborbicular, 11–14 × 12–14 mm, adaxial surface sericeous, base cordate, claw 1.0–1.5 mm long; wings obovate, 9–12 × 4.5–6.0 mm, distally pilose, without sculpturing, claw 1.5–2.0 mm long; keel cymbidiform, 8–10 × 4.5–5.5 mm, pilose on lower margin, claw 1.5–2.5 mm. *Stamens* monadelphous, sheath fused above. *Pistil* narrowly oblong; ovary 6–8 × 1–2 mm; style 3–4 mm long. *Fruit* rufous-pilose, compressed, up to 45 × 5 mm. *Seed* subglobose, laterally compressed, 2.5–3.0 mm in diameter, yellow to light brown, hilar rim raised.

Floral dimensions in the description refer to chasmogamous flowers. Cleistogamous flowers are of no use in species delimitation.

A. rotundifolium (Figure 9) is allied to *A. rupestre* but is distinguished by its consistently prostrate habit (*A. rupestre* is better described as ascending or decumbent), broadly elliptical to orbicular leaflets, shortly rufous-tomentose indumentum and the lack of sculpturing on its wing petals. This species is predominantly coastal in

distribution whereas *A. rupestre* is limited to inland areas (Figure 10). In southern Natal *A. rupestre* approaches the coast on the high lying areas around Kokstad and Harding, however, no contact zones with *A. rotundifolium* have been observed.

NATAL.—2731 (Louwsburg): Itala Nature Reserve, (—CA), *Germishuizen 2232* (PRE). 2831 (Nkandla): Ngoye, (—DC), *Huntley 852* (NU). 2832 (Mtubatuba): Hluhluwe Game Reserve, Mbhombe, (—AA), *Hutchins 598* (NH, NU). 2931 (Stanger): Nonoti Lagoon, (—AD), *Ward 9121* (PRE). 3030 (Port Shepstone): Oribi Gorge, Riverview, (—CA), *Van Wyk 5064* (PRE). 3130 (Port Edward): 7 km from Port Edward on the Izingolweni Rd, (—AA), *Hilliard 1738* (NU).

CAPE.—3228 (Butterworth): The Haven, (—BA), *Gordon-Gray 557* (GRA). 3229 (Talemofu): Hole in the wall, (—AA), *Germishuizen 1860* (PRE).

***Argyrobium lotoides* Harv.** in *Flora capensis* 2: 595 (1862). Type: Transkei, *H. Bowker 366* (TCD, holo.; K!, PRE! iso.). Figure 11.

A. variopile N.E. Br.: 18 (1906); B-E. van Wyk: 395 (1987) synon. nov. Syntypes: Natal, Volksrust, hillside near Charlestown, *Wood 5693* (BOL!, K!, NH!, PRE!), *Wood 6355* (K!, NH!, SAM!).

A. hirsuticaule Harms: 179 (1917) synon. nov. Type: Transkei, Zuurbergen, *Schlechter 6571* (B†, holo.; BOL, lecto.! selected here).

A. leptocladum Harms: 180 (1917) synon. nov. Type: Kokstad, around Clydesdale, *Tyson 1256* pro parte (B†, holo.; BM!, icono. selected here).

A. thodei Harms: 184 (1917) synon. nov. Type: Witzieshoek, *Thode 20* (B†, holo.; BM!, icono. selected here).

Lotononis magnistipulata Dümmer: 299 (1913). Type: Faku's Territory (probably Transkei), *Sutherland s.n.* (K, holo.).

Early collections of this species, made by Drège, bear the name *Chasmosyne pilosissima* but no published description was traced. The three names published by Harms were based on differences in vestiture and leaf dimensions. These highly variable characters form a continuum and are thus unsuitable for delimiting species. The specimens from which *A. leptocladum* and *A. hirsuticaule* were described were destroyed in Berlin. The drawings of these specimens at BM are therefore selected

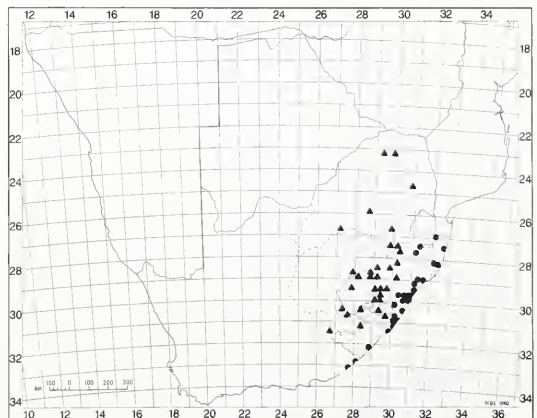


FIGURE 10.—The known distribution of *Argyrobium rotundifolium*, ●; and *A. rupestre*, ▲, in southern Africa.



FIGURE 11. — *Argyrolobium lotoides*, Browning 183 (NU). A, habit; B, dissected calyx, inner surface; C, standard, adaxial surface; D, wing; E, keel; F, androecium. Scale bars: A = 10 mm; B–F = 1 mm.

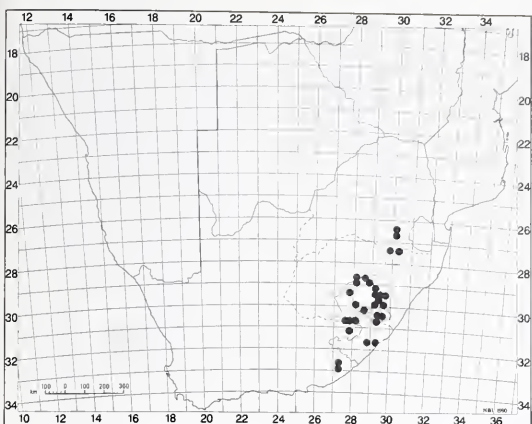


FIGURE 12.—The known distribution of *A. lotoides*, ●.

as iconotypes. The type of *A. leptocladum* is part of a mixed collection (Tyson 1256); unfortunately only specimens of *A. amplexicaule* remain from this gathering (these are listed below under additional specimens examined).

The species (Figure 12) occurs commonly in highland sourveld and is frequently associated with rocky outcrops.

TRANSVAAL.—2630 (Carolina): Chrissiemeer, (—AC), Theron 2383 (PRE). 2729 (Volksrust): hillside near Charlestown, (—BD), Wood 5693 (BOL, K, NH, PRE), Wood 6355 (K, NH, SAM).

ORANGE FREE STATE.—2828 (Bethlehem): Generaalskop, (—DA), Roberts 3298 (PRE).

NATAL.—2730 (Vryheid): Naauwhoeck, (—AD), Devenish 2124 (E, K, NU, PRE, S). 2929 (Underberg): Sani Pass, (—CB), Hilliard & Burt 15534 (E, NU, PRE); Browning 183 (NU). 3029 (Kokstad): Zuurberg near Weza, (—BC), Hilliard & Burt 8070 (E, MO, NU, PRE).

LESOTHO.—2927 (Maseru): Molmo Ntuse mountain road, (—BD), Schmitz 7248 (PRE). 2928 (Marakabei): Semonkong, (—CC), Jacot

Guillarmod 1812 (PRE). 3027 (Lady Grey): Ben McDhui, (—DB), Galpin 6607 (PRE).

CAPE.—3028 (Matatiele): Quachasnek, hillside facing Maluti Hotel, (—BA), Gordon-Gray 4042 (E, NU).

Additional specimens examined

Argyrobium amplexicaule

NATAL.—3029 (Kokstad): in hills around Clydesdale, (—BD), Tyson 1256 (BM, BOL, K, SAM, UPS).

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T.J. EDWARDS*

* UN/FRD Unit for Plant Growth and Development, Botany Department, University of Natal, P.O. Box 375, Pietermaritzburg 3200.
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ALLISONIACEAE

THE HEPATIC, *CALYCULARIA CRISPULA* (METZGERIALES) REPORTED FROM MALAWI AND ZAMBIA

Calycularia crispula Mitt., in *Journal of the Proceedings of the Linnean Society of Botany* 5: 122 (1861); Pandé & Udar: 331 (1956); Jones: 497 (1985). Type: Himalayas, Sikkim, J.D. Hooker 1679 (G, iso.).

Calycularia goliae Gerola: 471–485 (1947). Type: Abyssinia, Vondo, Vatova s.n.

Thallus procumbent, dark bottle-green, to olive-green, nearly translucent, delicate and easily torn when wet; almost colourless in dead basal parts, with brownish margins when dry; in overlying mats, on tree bark or on soil covering tree boles; firmly adherent to substrate along midrib throughout its length; 7.5–23.0 mm long, simple or with a single terminal bifurcation (Figures 13A; 14A), branches 5.0–7.5 × 7.5–9.0 mm, occasionally short lateral branches arising ventrally near base, basal part semi-lobate; wings thin and wide, margins slightly scalloped and strongly undulate, otherwise entire; apex notched (Figure 13E) with the 2 terminal lobes overlapping

somewhat; ventral scales situated between lobes and visible from above, arched over edge, small and inconspicuous, mostly confined to apices of ventral face, colourless, up to 500 µm long, 3 or 4 cell rows wide at base, central cell row longer and tapering to uniseriate tip, lateral rows shorter, all ending in and laterally with one to several slime papillae, ± 50 µm, with spherical top (Figure 13C); rhizoids very long and dense, smooth, faintly brown, ± 20 µm in diameter, restricted to midrib ventrally; midrib ± 1/5 of branch width, ± 280 µm (or more) thick and generally consisting of 12–15 rows of thin-walled homogeneous cells (Figure 13D), in cross section 4–6-sided, ± 42.5 × 27.5–32.5 µm, in longitudinal section ± rectangular, up to 137 µm long, without a central strand of conducting cells, gradually becoming thinner laterally and wings eventually unistratose (Figure 13D); epidermal cells of midrib slightly thicker-walled, rectangular to pentagonal, generally 55 × 25 µm, in cross section 32.5 × 25.0–32.5 µm, containing numerous chloroplasts, ± 5.0 µm

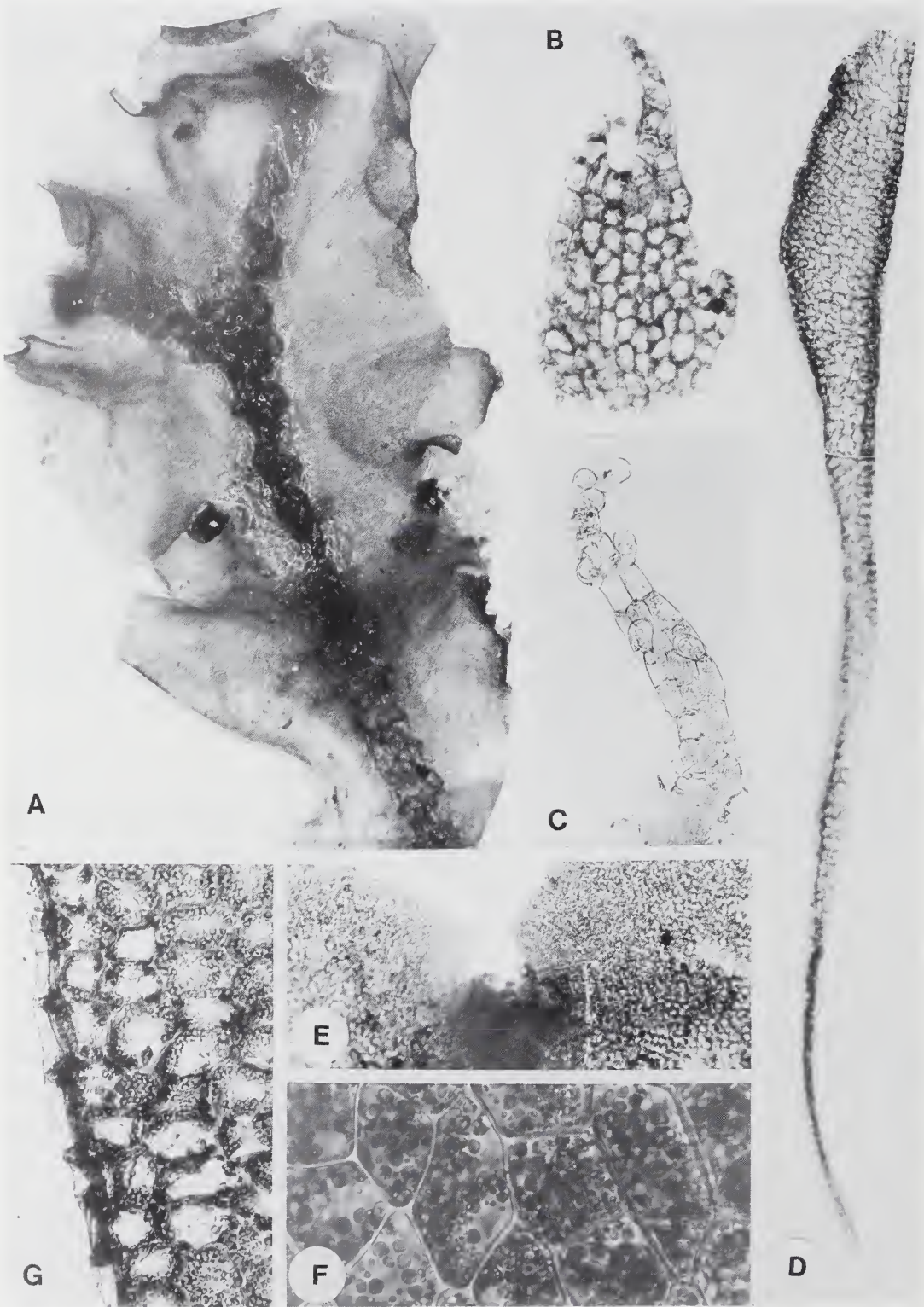


FIGURE 13 — *Calycularia crispula*. A, male thallus with androecia; B, scale-like involucre which individually covers antheridium; C, ventral scale with slime papillae; D, part of transverse section of thallus, showing one unistratose wing and costa without central conducting strand; E, ventral face of apex of thallus, showing apical notch and slime papillae; F, chloroplasts and small oil bodies inside thallus cells, seen from above; G, cells along margin of thallus seen from above. A–C, F–G, *S.M. Perold* 2677; D, *S.M. Perold* 2668. A, $\times 9.5$; B, $\times 90$; C, $\times 125$; D, E, $\times 45$; F, $\times 400$; G, $\times 150$.

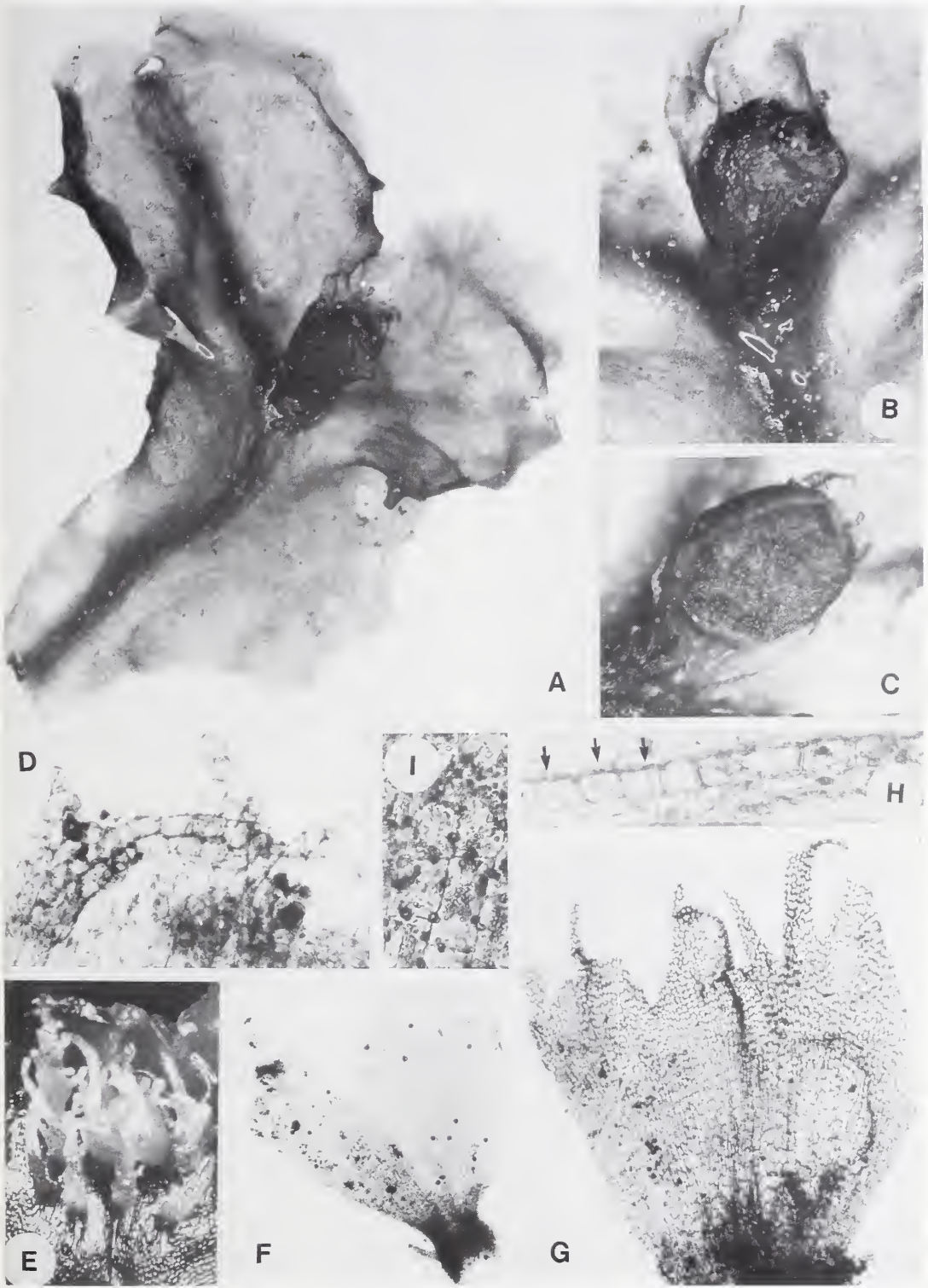


FIGURE 14.—*Calycularia crispula*. A, female thallus with young sporophyte enclosed in perianth; B, close-up of sporophyte; C, longitudinal section through capsule; D, involucral scales; E, cluster of archegonia protected by involucral scales, near apex of thallus; F, calyptra showing unfertilized archegonium at base; G, perianth with lacinate mouth; H, transverse section of capsule wall, rod-like thickenings indicated by arrows; I, cells in fragment of capsule wall, thickenings from above seen as dots. A–I, *S.M. Perold* 2668. A, $\times 6.5$; B, C, $\times 12$; D, $\times 90$; E, $\times 20$; F, G, $\times 18$; H, I, $\times 300$.

in diameter, as well as small oil bodies (Figure 13F); cells in wings, from above, pentagonal or hexagonal, $45\text{--}50 \times 30\text{--}50 \mu\text{m}$; cells at margin rectangular, $32.5\text{--}57.5 \times 17.5\text{--}22.5 \mu\text{m}$ or pentagonal, $25 \times 30 \mu\text{m}$ (Figure 13G).

Dioicous. *Androecia* consisting of 3 or 4(5) crowded, \pm parallel rows of male scales overlying the midrib in the body of the thallus, reduced to 2 rows in the terminal branches (Figure 13A), antheridia short-stalked, globular, $\pm 250 \times 240 \mu\text{m}$ when mature, each one covered by a forwardly directed laciniate scale (Figure 13B, C), laciniae up to $550 \mu\text{m}$ long $\times 250 \mu\text{m}$ wide at base, composed of cells $45\text{--}75 \times 45 \mu\text{m}$. *Gynoeceia* acropetally arranged and singly placed dorsally, near the notched apex and when present, above the furcation of the branches (Figure 14A, B), slightly raised on a swelling, each with a group of $\pm 6\text{--}11$ young archegonia (Figure 14E), $\pm 325 \mu\text{m}$ long, the necks composed of 6 cell rows and the tips brownish; just posterior to the archegonia and at their sides subtended by an involucre of narrow, laciniate scales (Figure 14D), erect to somewhat forwardly directed; when mature, the capsule spherical to ovate, leaning obliquely forward, $1750 \times 1500 \mu\text{m}$, containing a mass of spores and elaters and raised on the seta, here only $\pm 1000 \mu\text{m}$ long (Figure 14C) and not maximally elongated; capsule wall brown, bistratose (Figure 14H), cells square or rectangular, 37.5×37.5 to $75 \times 20 \mu\text{m}$, cell walls thin, but with some conspicuous orange-coloured semi-annular bands or stiffening rods, the latter projecting into the cell lumen (Figure 14I); perianth obconic and large when mature, enclosing capsule, green, with laciniate mouth (Figure 14G), $3100 \mu\text{m}$ long including $\pm 600 \mu\text{m}$ long laciniae, cells $\pm 75.0 \times 37.5 \mu\text{m}$; calyptra delicate and transparent (Figure 14F), bistratose, cells mostly pentagonal, $\pm 50.5 \times 37.5 \mu\text{m}$, with unfertilized archegonia attached to base. *Spores* with distal face rounded (Figure 15C, D), proximal

face flat or indented (Figure 15A), light brown, translucent, diameter $35.0\text{--}42.5 \mu\text{m}$, densely echinate, spines occasionally rather blunt, straight or bent (Figure 15B), $7.5 \mu\text{m}$ long and $5.0 \mu\text{m}$ wide at base, in between them small projections arising at corners of shallow areolae. *Elaters* bispiral (Figures 15F; 16), $10.0 \mu\text{m}$ thick, $\pm 310 \mu\text{m}$ long, tips solid, rounded. *Vegetative reproduction* by stipe arising from group of cells in colourless, seemingly dead marginal or basal parts of thallus, almost lunate, $175 \times 375 \mu\text{m}$, soon narrowly winged; also by ventral branches arising from midrib.

Grows on tree trunks and apparently also on soil, in sheltered, damp places in montane forest.

DISCUSSION

Calycularia crispula (family Allisoniaceae, order Metzgeriales) is well known in the Himalayas. An excellent description and line drawings of Indian material were given by Pandé & Udar (1956), who also studied the ontogeny of the gametangia and the embryogenesis. Jones (1985) remarked that his records of *C. crispula* were only the second report of this species from Africa [Tanzania and Malawi (which includes part of Chowo Forest)], the first was by Gerola (1947), when he described *C. golae* from Ethiopia (= Abyssinia). Jones believed that this species should be treated as a synonym of *C. crispula*. Arnell (1960) had misidentified a specimen of *C. golae*, collected by Dr John Eriksson in Ethiopia (= Abyssinia), as *Monocolea gottschei* Lindb. (Grolle 1985), which does not, however, grow in Africa. Besides the Himalayas (and Indomalaya) the genus *Calycularia* is also known from Taiwan, Japan, Siberia, Alaska (Schuster 1982), the Aleutian Islands and Pacific northwest of North America (Davidson & Smith 1992), as well as Mexico (Grolle 1980), and it is probably of Laurasian origin. Although

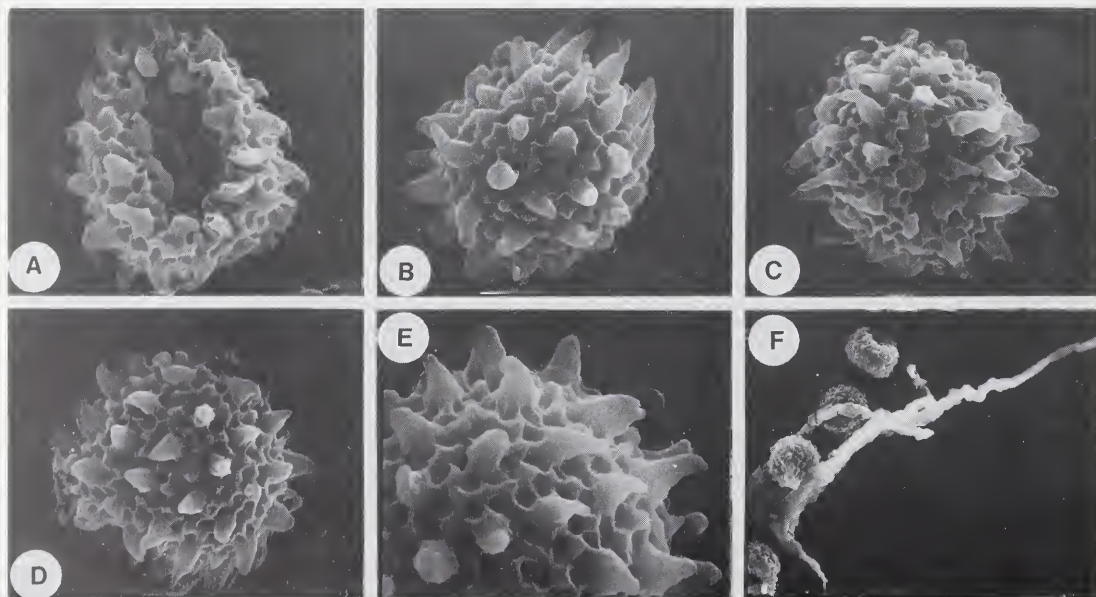


FIGURE 15. — *Calycularia crispula*. SEM micrographs of spores. A, ?proximal face of spore; B, spore seen from side; C, D, distal face of spore; E, part of spore much enlarged; F, young spores and elaters. A–E, S.M. Perold 2668; F, S.M. Perold 2677. A–D, $\times 995$; E, $\times 1990$; F, $\times 260$. Micrographs by S.M. Perold.



FIGURE 16.—*Calycularia crispula*, LM photograph of elater, S.M. Perold 2677, $\times 350$.

Stephani (1900) had assigned six species to the genus, it now appears to have just two, with *C. crispula* and *C. laxa* Lindb. & Arnell [confined to the polar regions of Alaska and Siberia (Davidson & Smith 1992)], the only species belonging here, because Schuster (1982) transferred *C. radiculosa* to the new monotypic genus, *Sandeothallus* Schust.

The specimens collected by me are appreciably smaller than the thallus sizes reported by Jones (1985), i.e. 20–50 mm long. My collections must be young plants, as only one mature sporangium was found, which had not yet dehisced. Pandé & Udar (1956) reported it as dehiscing by 4–6 irregular valves. An elaterophore was not observed either; apparently it is not well developed in this species. The seta did not elongate much and the sporangium remained inside the perianth; with maturity the seta reportedly elongates and raises the sporangium above the perianth. The antheridia may not always be in continuous rows and may grow in groups. The small ventral scales are mostly confined to the region close to the apices of the plants examined; their presence distinguishes *Calycularia* from *Pallavicinia lyelli* and *Dumortiera hirsuta*, which lack them. The SEM spore micrographs taken in this study compare well with those of Inoue & Hibino (1984).

Specimens examined

ZAMBIA.—1033: Nyika Nat. Park, (–DA), Chowo Forest, on bark of tree next to path, 15-4-1991, S.M. Perold 2668.

MALAWI.—1033: Nyika Nat. Park, (–DA), 15 km W of Chilinda, in forest on *Parinari excelsa* tree, 16-4-1991, S.M. Perold 2677.

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S.M. PEROLD

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First report on the presence of *Enterobryus* species (Trichomycetes: Eccrinales) in South Africa and the description of three new species

G.J.M.A. GORTER*

Keywords: Diplopoda, Eccrinales, *Enterobryus* spp. nov., gut fungi, millipedes, South Africa, Trichomycetes

ABSTRACT

The occurrence of Trichomycetes in the Republic of South Africa is reported for the first time. Thus far only various juliform millipedes have been examined for the presence of these fungi. Three new species of *Enterobryus* have been found and are described in detail, viz. *E. centroboli* Gorter, *E. chaleponci* Gorter and *E. zinophorae* Gorter.

UITTREKSEL

Die voorkoms van Trichomycetes in die Republiek van Suid-Afrika word vir die eerste keer aangemeld. Tot dusver is slegs verskillende wurmagtige duisendpote vir die aanwesigheid van hierdie swamme ondersoek. Drie nuwe spesies van *Enterobryus* is gevind en word beskryf, nl. *E. centroboli* Gorter, *E. chaleponci* Gorter en *E. zinophorae* Gorter.

INTRODUCTION

Enterobryus species are gut fungi which belong to the class Trichomycetes, lower fungi which are placed in the Subdivision Zygomycotina (Lichtwardt 1986). All Trichomycetes are characterised by the production of sporangiospores and the presence of a secreted holdfast with which the thalli are attached, mostly to the internal cuticular surface of certain Arthropoda. Four orders have been recognised in the Trichomycetes by Manier & Lichtwardt (1968), viz. Harpellales, Asellariales, Eccrinales and Amoebidiales. Sexual reproduction has been observed only in the Harpellales and in one genus (*Enteropogon*) of the Eccrinales (Hawksworth *et al.* 1983). None of these fungi have been grown in axenic culture except a few of the Harpellales (*Smittium* spp. and *Trichozygospora chironomidarum*) and one of the Amoebidiales (*Amoebium parasiticum*) (Lichtwardt 1978). However, this does not imply that they are parasites. Their relationship with their hosts is considered to be commensalistic, the host neither benefitting nor suffering from the association (Moss 1979). They produce one or more types of sporangiospores basipetally. Lichtwardt (1954, 1958) designated these spore types as A, B, C, D, E, F and G. They are attached by a holdfast to the hindgut cuticle of Diplopoda, less often Insecta (Coleoptera) and Crustaceae (Lichtwardt 1986). As noted by Lichtwardt (1978), the Eccrinales is, from a taxonomic viewpoint, the most difficult order of the Trichomycetes to study, probably on account of the unstable morphology of its members and the inability of researchers to culture them.

Work on the Eccrinales has been done principally in Europe, particularly in France (Dubosq *et al.* 1948; Manier 1950, 1954, 1961, 1963, 1964, 1969, 1970; Poisson 1927, 1928, 1929, 1931) and in the United States of America (Leidy 1849a, b; Lichtwardt 1954, 1957a, b, 1958, 1960a, b), but studies have also been done in India (Rajagopalan 1967) and Japan (Lichtwardt *et al.* 1987).

This article records the presence of these fungi for the first time in South Africa.

MATERIALS AND METHODS

Fungi for study were obtained from live Diplopoda. The procedures for dissection of the millipedes and observation for the presence of fungi were similar to those used by Lichtwardt (1954). However, to facilitate the cutting off of the head and anal segment, the live millipedes were first immobilised by placing them in tubes of a suitable dimension and cooling them in a freezer for 10 or more minutes, depending on the size of the millipede. The gut was then removed by grasping the posterior portion of the hindgut with a forceps and gently pulling the gut from the body. Next, the gut was cut open with finely pointed, curved scissors after which the undigested gut content was removed with the aid of a thin jet of water. As the removal of the cuticle with the fungi from the gut was found to be laborious and not always successful, most examinations were made of the fungi *in situ*, either in water or after treatment with lactophenol, with or without cotton blue. Observations on nuclei were made after fixing in Clarke's fluid (Bradbury 1973) and staining with Heidenhain's iron-alum-haematoxylin.

Millipedes were obtained from various parts of the country. Studies were confined to the juliform type of millipedes.

RESULTS AND DESCRIPTIONS

During the rainy seasons of 1989/90 and 1990/91, dozens of millipedes of different species including common ones such as *Dorotogonus setosus* (Voges), *D. circulus* (Attems) and *Orthoporoides pyrocephalus* (L. Koch), were examined for the presence of Trichomycetes. Every species showed some signs of infestation. However, most of them lacked primary spores whereas the mycelium with secondary spores had traits similar to those described species which produce primary spores. This has made identification impossible. Nevertheless, in different groups of

* Plant Protection Research Institute, Private Bag X134, Pretoria 0001. MS. received: 1992-02-II.

millipedes, three fungi were encountered which differed sufficiently from described species to be recognised as new.

Figures illustrating the newly described species serve as holotypes because the slides on which they are based are subject to deterioration.

Enterobryus centroboli Gorter, sp. nov.

Hyphae rectae vel undulatae, 3000–3800 \times 7.5–12.5 (–15) μ m, plerumque hyalinae. Cytoplasma granulosum et obscurum in hyphis laterioribus. Hyphae saepe tumidae prope basim sed angustiores ad retinaculum. *Retinaculi* orbis basalis 10.0–12.5 (–15) μ m diam., caulis perbrevis, circa 5.0 \times 7.5 μ m, vel absens. *Sporangiosporae* (typus A) 15.0 \times 7.5 μ m (uninucleatae) et 40–60 \times 7.5 μ m (quadrinucleatae). Sporae multinucleatae (typus E) 90–125 \times 10–20 μ m. Sporae uninucleatae (typus F), 5.0–7.5 \times 10 μ m.

Habitat affixa in intestino posteriore *Centroboli* spp., Natal, 1991.

TYPUS.—Figura 1A–F nititur laminis vitreis PREM 50874 (NC 20), PREM 50875 (NC 18) et PREM 50876 (NC 43) *Centroboli lawrencei* (Schubart).

The fungus develops unbranched thalli which are attached to the anterior part of the hindgut, just below but occasionally also just inside the sphincter muscle (the muscle which divides the fore- and hindgut). Hyphae also develop towards the posterior end of the hindgut. In both cases, the hyphae are fairly straight to undulating, 7.5–12.5 (–15) μ m wide, those at the front are up to 3800 μ m long and those at the back up to 3000 μ m. Most hyphae are hyaline but some of those in front tend to become wider and more opaque as the result of dense granular cytoplasm towards the hyphal apex. The narrower hyaline hyphae produce at their apex short or longer type A sporangiospores. The short ones (15.0 \times 7.5 μ m) are uninucleate and the longer ones (40–60 \times 7.5 μ m) are quadrinucleate (Figure 1A, C). The wider, more opaque hyphae produce 3 to 4 apical or sometimes intercalary spores, 90–125 \times 10–20 μ m (Figure 1F), which appear to be multinucleate and of Lichtwardt's type E.

Holdfasts are produced at the straight basal ends of the hyphae which are often swollen (by 2.5–5.0 μ m) towards the holdfast and then narrow towards the point of attachment (Figure 1E). The holdfast has a very short stalk which is often shorter than wide, e.g. 5.0 \times 7.5 μ m. The diameter of the attachment disc is comparatively small, viz. 10.0–12.5 (–15) μ m.

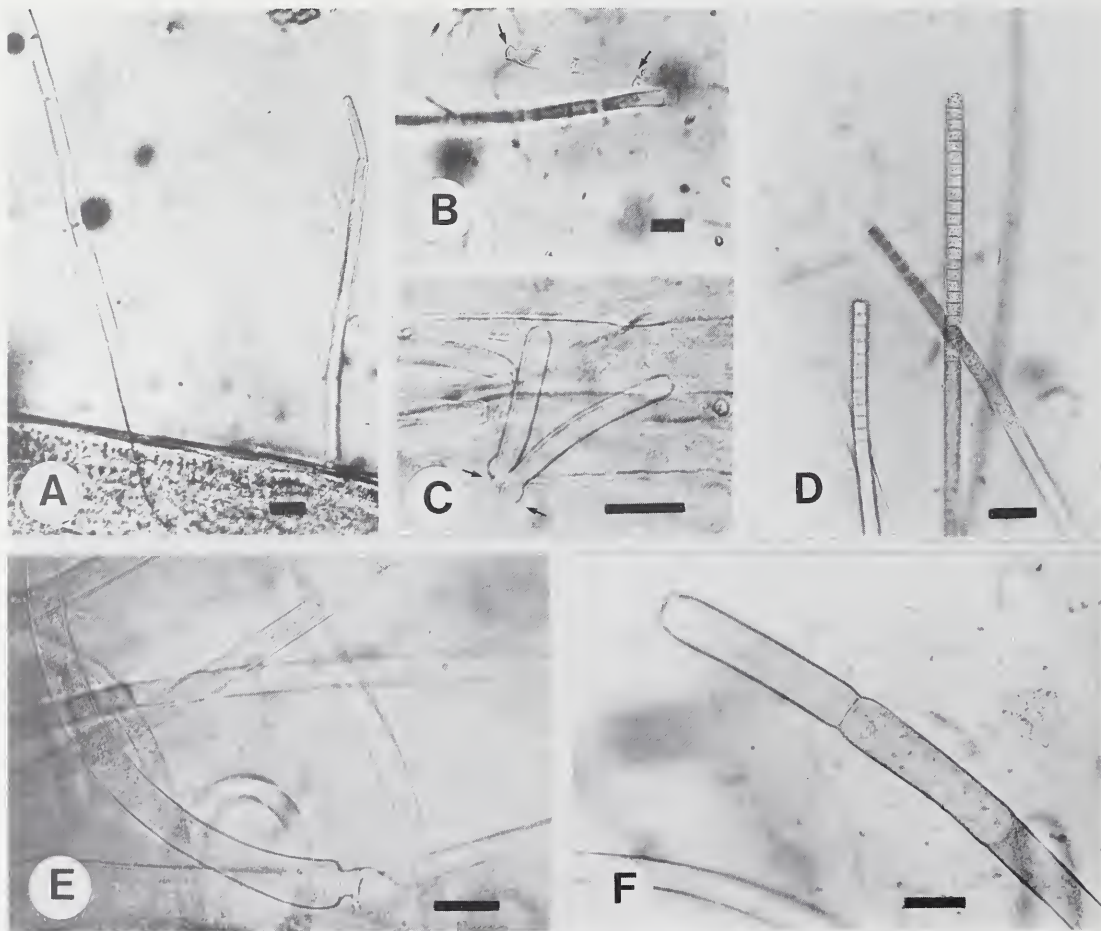


FIGURE 1.—*Enterobryus centroboli* Gorter. A, left, hyphae with 4-nucleate A spores, right, germinated type A spore fastened to substrate; B, empty sporangia (arrowed) from which type A spores have escaped; C, germinated type A spores which immediately develop holdfasts (arrowed); D, stacks of uninucleate primary spores; E, base of hypha which widens towards holdfast; F, type E spores. Scale bars = 25 μ m.

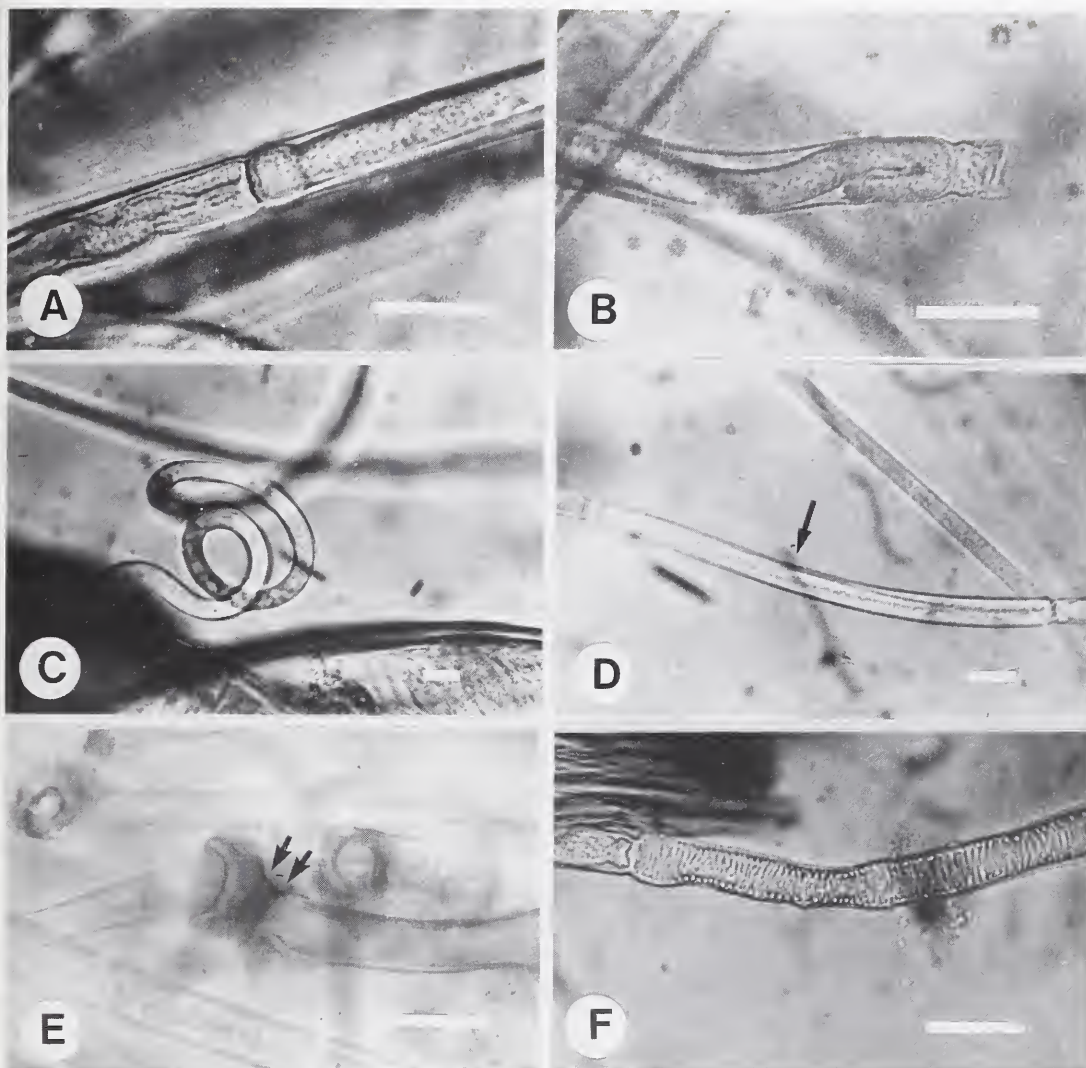


FIGURE 2.—*Enterobryus zinophorae* Gorter. A, rounded base of folded spore inside basal part of sporangium; B, apex of developing folded spore; C, spiral base of hypha devoid of sporangia; D, mature folded spore inside sporangium in straight part of hypha (spore tip arrowed); E, holdfast with short stalk (arrowed) on base of straight hypha; F, empty sporangium cell with transverse folds in wall. Scale bars = 25 μ m.

Hyphae which produce primary sporangiospores are rare or absent. These hyphae are found at the posterior end of the hindgut where they produce stacks of up to 85 uninucleate spores towards their apex (type F) which are slightly shorter than wide, viz. $5.0\text{--}7.5 \times 10 \mu\text{m}$ (Figure 1D). Here, too, the holdfast has a short stalk, up to 5 μm , with a small disc diameter of $10.0\text{--}12.5 \mu\text{m}$.

Habitat: attached to the hindgut lining of *Centrobolus* spp. from Natal (Cedara and Mtunzini), 1991.

TYPE.—Figure 1A–F, based on slides PREM 50874 (author's collection number NC 20), PREM 50875 (NC 18) & PREM 50876 (NC 43) all of *Centrobolus lawrencei* (Schubart).

Enterobryus zinophorae Gorter, sp. nov.

Hyphae rectae, flexae vel undulatae, $2000\text{--}3000 \times (7.5\text{--})10.0\text{--}12.5\text{--}(15) \mu\text{m}$, raro incurvatae prope basim.

Cytoplasma hyalinum. Hyphae leviter dilatatae ad basim. Retinaculum cum caule brevissimo, brevior quam lato, haud longior quam 6 μm ; orbis basalis $12.5\text{--}20.0 \mu\text{m}$ diam. Nonnullae hyphae 1–6 cellulas sporangiales $175\text{--}300 \times 10 \mu\text{m}$ ad apicem producentes. Sporangia matura sporam unam longissimam replicatamque continentia. Sporae basi tumida et rotunda sine palliolo apicali. Post liberationem sporarum parietes sporangiales contrahuntur fiuntque multirugosi. Sporae liberatae, $250\text{--}350 \times 7.5\text{--}10 \mu\text{m}$, a fundo germinantes, hyphas breves cum retinaculo producentes. Formas alias sporarum non vidi.

Habitat affixa intra sphincterem intestini *Zinophorae* spp.

TYPUS.—Figura 2A–F nititur laminis vitreis PREM 50877 (MP 4) et PREM 50878 (MP 7) *Zinophorae dipodontae* (Attems), Pretoria, Transvaal, Dec. 1990.

The thalli are inside the sphincter muscle. The hyphae are hyaline, straight, bent or undulating towards their apex but occasionally hooped near their base (Figure 2C), 2000–3000 \times (7.5–)10.0–12.5(–15) μ m. Hyphae have rounded ends and may widen slightly towards their base where they secrete a holdfast with a short stalk not longer than 6 μ m and usually shorter than wide (Figure 2E). Some hyphae produce a number of cells 175–300 μ m long and usually 10 μ m wide towards their apex. These are sporangia which, when mature, contain long, folded spores (Figure 2B, D) with a slightly swollen obtuse base (Figure 2A) and a pointed apex without a protecting cap as illustrated by Manier *et al.* (1974: fig. 1F). These spores are 250–350 \times 7.5–10.0 μ m. The sporangia, from which they escape, contract to become empty cells with many folds (Figure 2F). The escaped spores straighten out, immediately develop a hypha from the rounded base and

attach themselves to the sphincter lining. The hypha keeps on growing after which the spore presumably degenerates (empty filaments at the end of comparatively short hyphae have been noted). No other type of spore has been observed.

Habitat: attached to the sphincter muscle lining of *Zinophora* spp.

TYPE.—Figure 2A–F, based on slides PREM 50877 (author's collection number MP 4) & PREM 50878 (MP 7) of *Zinophora diplodonta* (Attems), Pretoria, Transvaal, Dec. 1990.

***Enterobryus chaleponci* Gorter, sp. nov.**

Hyphae hyalinae, satis rectae sed plerumque circulares prope basim, circa 2500 \times (10.0–)12.5–15.0(–17.5) μ m, in circulis plerumque latiores quam alibi; latitudo

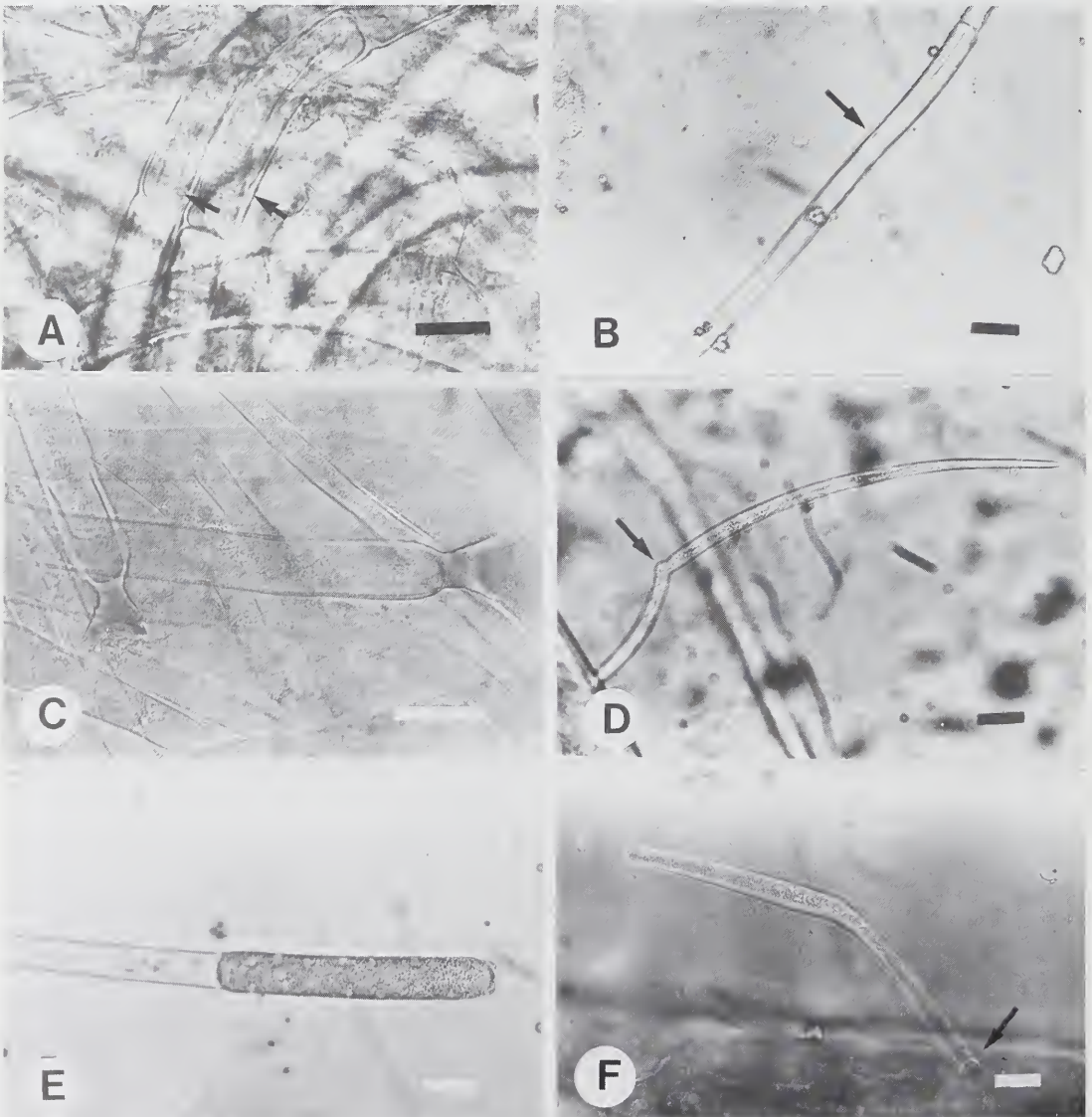


FIGURE 3.—*Enterobryus chaleponci* Gorter. A, short sporangia with folded spores (tips arrowed) inside hoops of swollen hyphae; B, mature spore inside sporangium in straight part of hypha (spore tip arrowed); C, holdfasts without stalks on straight basal end of hyphae; D, germinated, straightened-out acicular spore (base arrowed); E, multinucleate spore of type E; F, germinated multinucleate spore attached to substrate (holdfast arrowed). Scale bars = 25 μ m.

aliquando etiam variat in partibus rectis. *Retinaculum* sine caule, vel cum caule perbrevis; orbis basalis (12.5–)15–20 μm diam. *Sporae* longissimae, 125–230 μm , sine palliolo apicali, replicatae, in sporangiis intra circulos 70–85 \times 15 μm , in partibus rectis 105–150 \times 12.5 μm . Fundus basalis spora truncatus cum levi depressione in centro. Cytoplasma hypharum latiorum dense granulosum prope apicem. Hyphae latae aliquando cellulas longas (ad 125 μm) producentes endosporium singulum multinuclearem continentes.

Habitat affixa intra sphincterem intestini *Chaleponci polechanci* Kraus, Baltimore, Transvaal, Mai. 1991.

TYPUS. — Figura 3A–F nititur laminis vitreis PREM 50879 (TB 5) et PREM 50880 (TB 30).

The thalli are inside the sphincter muscle. The hyphae are hyaline, fairly straight but strongly hooped lower down, $\pm 2500 \times (10\text{--})12.5\text{--}15.0\text{--}(17.5) \mu\text{m}$. The hoops are often wider than the straight parts of the hyphae, 15–20 μm . The latter are of variable width, widening by 2 μm and then narrowing again. A holdfast (Figure 3C) without a stalk or with a very short one, e.g. 2.5 μm , develops at the base of a hypha. The disc diameter varies from (12.5–)15–20 μm . The thicker hyphae and those that widen from bottom to top, have a dense granular cytoplasm and often become slightly brown. Folded spores have been observed in the hooped as well as the straight part of hyphae (Figure 3A, B). In the first, sporangia are 70–85 \times 15 μm ; in the latter, 105–150 \times 12.5 μm . The spores are 125–230 \times 10.0–12.5 μm and have a truncated basal end with a slight depression in the centre. After escaping from the sporangia, the folded spores straighten, germinate basally and soon attach themselves to the inside of the sphincter muscle (Figure 3D). At the apex of a hypha with dense cytoplasm, a long cylindrical sporangium (up to 125 μm) is often formed (Figure 3E). These sporangia are slightly swollen in comparison with the rest of the hyphae and each contains a multinucleate endospore.

Habitat: attached to the sphincter muscle lining in the gut of *Chaleponcus polechancus* (Kraus), Baltimore, Transvaal, May 1991.

TYPE. — Figure 3A–F, based on slides PREM 50879 (author's collection number TB 5) & PREM 50880 (TB 30).

DISCUSSION

Apart from reporting the occurrence of Trichomycetes for the first time in South Africa, a most interesting result of this investigation was the discovery of sporangia containing long, folded, pointed spores in some of these fungi. These have hitherto been found only in millipedes from Central Africa by Manier *et al.* (1974/75). They described a number of species in which acicular, folded spores are formed but noted that they develop only in the narrow hyphae. This led Lichtwardt (1986) to pose the question of whether the thalli with long, folded spores perhaps belong to one fungal species, whereas the wider thalli with different spores belong to different fungi. The latter supposition is apparently supported by our finding that, in *E. chaleponci*, the two types of spores present mostly occurred alone in different specimens of a batch

of 36 millipedes of this species from one locality. However, the fact that these spore types were found together, albeit infrequently, and the fact that narrow hyphae could enlarge to become wider, point to a close relationship.

The suggestion that hyphae with long, folded spores all belong to one species is probably not valid because I found clear differences in size between the folded spores of *E. chaleponci* and *E. zinophorae*. The shape of their basal ends also differed slightly while they develop at a different locus. In *E. zinophorae* they develop only in the straight part of hyphae, while in *E. chaleponci* also within the hooped part of hyphae. Furthermore, Manier *et al.* (1974/75) observed that in some Eccrinales species the apex of the folded spore is protected by a solid point devoid of protoplasm, whereas in other species this protection is absent. These differences all indicate that different species are involved.

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Mycorrhizal status of plants growing in the Cape Floristic Region, South Africa

N. ALLSOPP* and W. D. STOCK*

Keywords: cluster roots, Fynbos, mediterranean-type shrublands, mycorrhizas, root systems

ABSTRACT

A survey of the mycorrhizal status of plants growing in the Cape Floristic Region of South Africa was undertaken to assess the range of mycorrhizal types and their dominance in species characteristic of this region. Records were obtained by examining the root systems of plants growing in three Cape lowland vegetation types, viz. West Coast Strandveld, West Coast Renosterveld and Sand Plain Lowland Fynbos for mycorrhizas, as well as by collating literature records of mycorrhizas on plants growing in the region. The mycorrhizal status of 332 species is listed, of which 251 species are new records. Members of all the important families in this region have been examined. Mycorrhizal status appears to be associated mainly with taxonomic position of the species. Extrapolating from these results, we conclude that 62% of the flora of the Cape Floristic Region form vesicular-arbuscular mycorrhizas, 23% have no mycorrhizas, 8% are ericoid mycorrhizal, 2% form orchid mycorrhizas, whereas the mycorrhizal status of 4% of the flora is unknown. There were no indigenous ectomycorrhizal species. The proportion of non-mycorrhizal species is high compared to other ecosystems. In particular, the lack of mycorrhizas in several important perennial families in the Cape Floristic Region is unusual. The diversity of nutrient acquiring adaptations, including the range of mycorrhizas and cluster roots in some non-mycorrhizal families, may promote co-existence of plants in this species-rich region.

UITTREKSEL

'n Opname van die status van mikorisas by plante wat in die Kaapse Floristiese Streek van Suid-Afrika voorkom, is onderneem om die omvang te bepaal van verskillende mikorisa-tipes en hulle oorheersing in spesies kenmerkend van hierdie streek. Rekords is verkry deur die wortelsisteme van plante in drie laagliggende Kaapse veldtipes, naamlik Weskus-strandveld, Weskus-renosterveld en Sandvlakte-fynbos, vir mikorisas te ondersoek. Rekords uit die literatuur van toepassing op mikorisas wat op plante in hierdie streek groei, is ook in ag geneem. Die status van mikorisas by 332 spesies word vermeld, 251 daarvan nuwe rekords. Lede van al die belangrike families in die streek is ondersoek. Die status van mikorisas is skynbaar hoofsaaklik met die taksonomiese posisie van die spesie geassosieer. Ons het tot die gevolgtrekking gekom dat 62% van die flora van die Kaapse Floristiese Streek vesikulêr-arbuskulêre mikorisas vorm, 23% geen mikorisas het nie, 8% erikoïede mikorisas vorm, 2% orgiïede-mikorisas het, terwyl die mikorisa-status van 4% van die flora onbekend is. Daar was geen inheemse spesies wat ektomikorisas gevorm het nie. Die proporsie nie-mikorisaspesies is hoog in vergelyking met dié wat in ander ekosisteme aangetref word. Die afwesigheid van mikorisas by verskeie belangrike meerjarige families in die Kaapse Floristiese Streek is veral ongewoon. Die verskeidenheid aanpassings om voedingsstowwe te bekom, insluitend die omvang van mikorisas en troswortels by sekere nie-mikorisafamilies, mag die gelyktydige bestaan van plante in hierdie spesie-ryke streek bevorder.

INTRODUCTION

It is generally accepted that most terrestrial plants probably form mycorrhizal associations between their roots and certain fungi, although the vast majority of plants growing in natural ecosystems have not had their mycorrhizal status confirmed (Trappe 1987; Newman & Reddell 1987). The mycorrhizal status of plants reflect both their taxonomic affinities and their ecology. Investigations on the mycorrhizal status of plants in various parts of the world indicate that the major terrestrial biomes can be characterized by specific mycorrhizal types (Read 1991). Surveys of mycorrhizas show that trees of forests and woodlands are either ectomycorrhizal or vesicular-arbuscular mycorrhizal; herbaceous plants and shrubs in grasslands and shrublands usually form vesicular-arbuscular mycorrhizas; boreal and temperate heathlands are dominated by ericoid mycorrhizal species; and disturbed ecosystems by non-mycorrhizal weed species (see Brundrett 1991 for references). Whereas the mycorrhizal status of some floras is well documented (e.g. British

Isles by Harley & Harley 1987), little is known about both the mycorrhizal associations of plants in the Cape Floristic Region (CFR) and their functional role in low nutrient ecosystems.

The vegetation of the CFR contrasts sharply, in terms of taxonomic composition and vegetation structure, with the surrounding southern African vegetation. The Cape flora has a high species diversity ($\pm 8\,500$ species), around 68% species endemism (Bond & Goldblatt 1984), and high beta and gamma species turnover (Cowling 1990). Agriculture, urbanization and alien plant invasion are a severe threat to this flora as a result of the limited range of many plant species, and have led to the destruction of much of the lowland vegetation (Hall 1983). Mycorrhizas act as soil nutrient-absorbing organs for the plants. As such they will influence the physiology of individuals, as well as their interactions with other plants growing in the same community (Harley 1989; Read 1991). Recognizing the patterns of distribution and understanding the ecological role of mycorrhizal types in a community may be crucial to understanding the dynamics which shape plant communities (Allsopp & Stock in press).

This study collates published records of the mycorrhizal status of plants occurring in the CFR as defined by

* Department of Botany, University of Cape Town, Private Bag, Rondebosch 7700, South Africa.
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Bond & Goldblatt (1984). In addition, the mycorrhizal status of plants growing in three lowland vegetation types, West Coast Strandveld, West Coast Renosterveld and Sand Plain Lowland Fynbos, is reported for the first time. The aim of this paper is to provide information on the mycorrhizal status of plant species which may be of significance in explaining vegetation patterns and plant functioning in the CFR.

STUDY AREAS

Three study sites representing West Coast Strandveld, at Melkbosstrand (33°45'S 18°27'E), West Coast Renosterveld on the hill, Joostenberg, on the farm Hercules Pillar (33°46'S 18°46'E), and Sand Plain Lowland Fynbos at the Fynbos Biome intensive study site (33°31'S 18°32'E) at Pella, were chosen to investigate the mycorrhizal status of a broad range of plants growing in threatened habitats in the CFR. The classification of the vegetation categories follows that of Moll *et al.* (1984). The strandveld vegetation, growing on coarse/medium sandy soil (organic matter 2.2%, pH of 7.5, total P 422 $\mu\text{g g}^{-1}$ (Witkowski & Mitchell 1987)) is a broad-leaved, sclerophyllous 1.0–2.5 m high shrubland with a large succulent component (Boucher 1983). The Renosterveld vegetation, growing on a fine sand/clayey soil [organic matter 4.9%, pH 4.1, total P 127 $\mu\text{g g}^{-1}$ (N. Allsopp unpublished)] is an evergreen, cupressoid or microphyllous shrubland, 1–2 m high, dominated by *Elytropappus rhinocerotis* with strong Lowland Fynbos affinities (Tansley 1982; Boucher 1983). The Sand Plain Lowland Fynbos growing on medium textured sandy soil [organic matter 1.4–3.4%, pH 4.6–4.8, total P 23–34 $\mu\text{g g}^{-1}$ (Mitchell, Brown & Jongsens-Roberts 1984)] is an ericoid-leaved, sclerophyllous vegetation, 0.75–1.5 m high with some taller shrubs, characterized by the presence of *Phylla cephalantha* (Boucher 1983). Vegetation surveys at the three sites have recorded 56, 63 and 215 perennial species at the Strandveld (Siegfried 1981), Renosterveld (Tansley 1982) and Lowland Fynbos (Boucher & Shepherd 1988) sites respectively. In addition annuals and bulbous species are numerically important components of all three vegetation types (Boucher 1983; Bond & Goldblatt 1984).

MATERIALS AND METHODS

Root collection

Roots were collected during August, September and early October when unthickened roots were common while the soil was moist. Two collections were made at both the Strandveld (during August 1987 and September 1989) and Renosterveld sites (during October in 1988 and September 1989). The Lowland Fynbos site was sampled six times over four years (June and August 1986, August and September 1987, September 1988, August 1989). Two 25 × 25 m plots were set up at a site on each collection day. The plots at the Strandveld site were situated 60–300 m inland of the high water mark. The Renosterveld plots were on the NW-SW-facing lower slopes of Joostenberg. At the Lowland Fynbos site, plots were randomly scattered throughout the 269 ha study site.

Roots of one representative of all species occurring in the plots were sampled. In addition, plant species not in the plots, but encountered in the vicinity, were sampled.

Smaller plants, including annuals, perennial seedlings and bulbous plants, were excavated with entire root systems. Roots of larger shrubs were collected by carefully tracing the root system from the main stem until young, unthickened roots were encountered. However, for some species, including members of the Anacardiaceae and Ebenaceae, few young roots could be found despite extensive excavation along roots down to 1 m. At the Renosterveld site some species were not sampled because they grew only in narrow cracks among rocks (e.g. *Olea* sp.). At the Strandveld site the large size of dominant shrubs and density of the vegetation at ground level, as well as spininess of some species, precluded collection of these species' roots.

Young roots were removed from surrounding soil in the field and immediately placed in vials containing 10% KOH for clearing. Wherever possible, 500 mm of root per plant was collected. Roots were cleared for one week at 20 °C, and then rinsed under running tap water (Smith & Bowen 1979). Where necessary, pigmented roots were decolourized with H_2O_2 or NaClO . This was followed by acidification in 1 M HCl and staining in 0.05% Trypan blue in lactic acid solution (Kormanik & McGraw 1982). Root segments were permanently mounted in a polyvinyl acid solution and inspected at 100 and 400 times magnification with a light microscope for mycorrhizal structures.

Plants were classified according to Cronquist (1988) and species names follow Gibbs Russell *et al.* (1985, 1987).

Literature survey

All known records of the mycorrhizal status of plants in the CFR were consulted. Only those records which reported the mycorrhizas of plants actually growing in the CFR are listed here. Confirmation of infection status of some species was undertaken by examining roots of plants growing in soil from their natural habitats in pot culture.

RESULTS

Vesicular-arbuscular mycorrhizas (VAM), characterized by the presence of arbuscules in the inner cortical cells with or without vesicles (Harley & Smith 1983), were the most common type of mycorrhiza (61% of species examined) (Appendix). Infections regarded as vesicular-arbuscular (VA) mycorrhizal but morphologically distinct from the above types were formed by *Aristea dichotoma*, which formed intracellular coils similar to those described by Brundrett & Kendrick (1990) in *Trillium grandiflorum*, while vesicular-arbuscular mycorrhizal fungi in *Orphium frutescens* and *Sebaea exacoides* formed structures typical of those seen in other members of the Gentianaceae (Jacquelinet-Jeanmougin & Gianinazzi-Pearson 1983). Infection formed by the 'fine endophyte' (Greenall 1963) was occasionally seen, but was never exclusively found on one species. Ericoid mycorrhizas (ERIC) were found in the hair roots of all members of the Ericaceae examined (Appendix). They are characterized by the formation of coiled and branched, fine hyphae in the cortical cells (Read 1983). Orchid mycorrhizas (ORCH) were seen in the two *Disa* spp. examined (Appendix) and consist of characteristic coarse, coiled intracellular hyphae (Harley & Smith 1983). No ectomycorrhizal infection was seen in the indigenous species examined. Introduced ectomycorrhizal

species such as pines, oaks, poplar and eucalypts form ectomycorrhizas in the CFR but the ectomycorrhizal fungi were in all likelihood introduced with imported saplings (Van der Westhuizen & Eicker 1987).

Ninety-one of the 332 species reported formed no mycorrhizas (Appendix). These were concentrated in the Caryophyllidae and the families Brassicaceae, Crasulaceae, Proteaceae, Santalaceae, Zygophyllaceae, Restionaceae and Cyperaceae. Plant roots which contained occasional vesicles but no arbuscules were regarded as functionally non-mycorrhizal (Hirrel *et al.* 1978).

Some earlier studies (Laughton 1964; Low 1980) have reported endophytic mycorrhizas (ENDO) as being present but descriptions or illustrations do not indicate structures which are typical of mycorrhizas as they are presently delimited (Harley & Smith 1983). Non-mycorrhizal fungi were fairly frequent in both mycorrhizal and non-mycorrhizal roots examined for this study. Therefore, reports of fungal infection as 'endophytic mycorrhizas' should be viewed with caution. The most common non-mycorrhizal root inhabiting fungus was *Olpidium* sp., which forms cysts and zoosporeangia (Sampson 1939), which may be mistaken for VA mycorrhizal vesicles if care is not taken. Unidentified hyphal fungi, including dark, septate hyphal fungi forming microsclerotia (DSH) similar to those described by Haselwandter & Read (1980) in alpine vegetation, were also present. The non-mycorrhizal roots of members of the Proteaceae have been shown to support a fungal flora that is distinctly different to that found in the non-rhizosphere soil (Allsopp *et al.* 1987). Infection by *Olpidium* sp. and other fungi was particularly heavy in the root systems of members of the Poaceae and Scrophulariaceae where they could obscure infection by VA mycorrhizal fungi (Appendix).

DISCUSSION

The mycorrhizal status of many of the taxa recorded here has not previously been reported, as can be expected, given the high levels of endemism and species radiation in the CFR and the paucity of mycorrhizal studies in this region. All the important families, as well as the twenty largest genera in the CFR (Bond & Goldblatt 1984), now have had some of their members examined for mycorrhizas. The endemic Penaeaceae and near endemic Bruniaceae have VA mycorrhizal species. Families which need further investigation are the Anacardiaceae, Ebenaceae, Juncaceae, and Celastraceae, as well as the endemic families Stilbaceae, Grubbiaceae, Roridulaceae, Retziaceae and Geissolomaceae. The lowland vegetation types have been well covered and generalizations regarding their mycorrhizas can now be made. However, the mycorrhizal status of the vegetation of habitats such as forests, seasonally waterlogged soils, limestone and mountain ecosystems are less well catalogued.

The absence of ectomycorrhizas is a notable feature of this flora. Ectomycorrhizal structures are reported in many plants growing in arid regions of Australia which belong to families and genera also present in the CFR (Warcup 1980; Warcup & McGee 1983; McGee 1986; Bellgard 1991). Ectomycorrhizas are also known to occur in the low nutrient soils of the Australian mediterranean heathlands (Chilvers & Pryor 1965; Brundrett & Abbott 1991). In

addition, ectomycorrhizas have been found on trees growing in other African ecosystems (Redhead 1968; Högborg & Pearce 1986). However, shrub vegetation growing on Kalahari sands adjacent to ectomycorrhizal woodlands was exclusively vesicular-arbuscular mycorrhizal (Högborg & Pearce 1986). The reasons for the exclusion of ectomycorrhizas from the CFR are not clear, although this can possibly be ascribed to the absence of an organic surface horizon which is usually associated with the presence of ectomycorrhizas (Read 1991), and to frequent disturbance by fire. For instance, in Italian mediterranean ecosystems on calcareous soils, canopy cover values for ectomycorrhizal plant species nine years after fire was a quarter of that in unburnt forest (Puppi & Tartaglini 1991). However, these explanations do not account satisfactorily for their absence in the CFR, because ectomycorrhizas occur in fire-prone communities in Australia with low soil organic matter (Brundrett & Abbott 1991).

The explosive speciation that the genus *Erica* has undergone in the CFR (± 530 spp.) implies that ericoid mycorrhizas are unusually common in this area. Cowling *et al.* (1990) have suggested that edaphic specialization of the endophyte has powered this speciation, but, as yet, supporting evidence is lacking. An interesting feature of ericoid mycorrhizal plants in the mediterranean-climate regions of the world is their co-existence with other plant species, whereas in more temperate regions they usually form almost pure stands in areas where soil degradation has produced soil conditions which plant roots and other mycorrhizas cannot tolerate (Leake *et al.* 1989).

All the non-mycorrhizal families in this study have been reported as such before, although some have had very few species examined for mycorrhizal colonization (Trappe 1987). Many of the non-mycorrhizal species in this study fall into the Caryophyllidae which is roughly equivalent to the Centrospermae (Cronquist 1988) which was originally regarded as non-mycorrhizal (Gerdemann 1968). Subsequent studies have shown that many species in this group are capable of forming mycorrhizas (Tester *et al.* 1987), and that some families are typically mycorrhizal, e.g. Cactaceae (Miller 1979). However, despite these exceptions, 80% of the species in the Caryophyllidae which have been examined are either non-mycorrhizal or facultatively mycorrhizal (Trappe 1987). Mechanisms which enable some species to actively exclude mycorrhizal fungi, when exposed to viable inoculum, are unclear (Tester *et al.* 1987; Koide & Schreiner 1992).

In dicotyledonous species, weedy, herbaceous plants often lack mycorrhizas or are weakly mycorrhizal (Malloch *et al.* 1980; Trappe 1987) and it has been noted that some species are less likely to form mycorrhizas when colonizing disturbed sites than adjacent undisturbed areas (Miller 1979; Reeves *et al.* 1979). In our study, the annuals in the Scrophulariaceae were usually non-mycorrhizal, although a few individuals form typical VAM.

Anaerobic conditions in waterlogged soils have been invoked to explain the absence of mycorrhizas in some plants (Anderson *et al.* 1984), and Tester *et al.* (1987) advance this as an explanation of the absence of mycorrhizas in most of the Cyperaceae. In this study the members of the Cyperaceae and the Restionaceae examined

were non-mycorrhizal while growing in well-drained soil with other mycorrhizal plants, although both families are often associated with waterlogged conditions, and so this does not seem to be the only reason for the exclusion of mycorrhizas from these taxa. Although Powell (1975) reported mycorrhizal structures in some roots of members of the Cyperaceae, he concludes that they are functionally non-mycorrhizal due to the possession of a fine root system. This complements Baylis' (1975) proposal that the magnolioid root form with poorly developed root hairs would be more strongly mycorrhizal than finer root systems. Two important perennial families in the CFR, which do not form mycorrhizas (viz. Proteaceae and Restionaceae), are characterized by the formation of cluster roots, the rootlets of which are densely covered in long root hairs (Purnell 1960; Lamont 1972a, 1982). In addition, cluster roots have been observed on members of the Cyperaceae (Lamont 1974), the genus *Aspalathus* (Fabaceae) (this paper and M. Cocks unpublished data) and Australian members of the Fabaceae (Lamont 1972b; Brundrett & Abbott 1991), which typically have low VAM infection levels. The absence or low infection levels of mycorrhizas in the taxa forming cluster roots support Baylis' (1975) proposition that mycorrhizas will be less important when root systems are finer. The loss of the ability to form mycorrhizas is regarded as an evolutionarily advanced feature (Trappe 1987).

The mycorrhizal status of the species in the CFR seems to be a reflection of their taxonomic position, although Newman & Reddell (1987) warn that very few families form exclusively one type of mycorrhiza or are consistently without mycorrhizas. This can be expected when worldwide the higher taxa of angiosperms are poorly correlated with their ecological niches (Cronquist 1988). Life form or environmental factors do not satisfactorily explain the absence of mycorrhizas in longer lived plants such as members of the Proteaceae, Restionaceae and Zygophyllaceae in the CFR and this must be regarded as a taxon-related characteristic for many groups. Reports of VA mycorrhizal species among the Proteaceae in New South Wales, Australia (Bellgard 1991) and ectomycorrhizal *Faurea saligna* (Proteaceae) in Zambia (Högborg & Pearce 1986), indicate that the mycorrhizal status of members of this family should be investigated with respect to soil fertility, as mycorrhizas are absent in members of this family growing in low nutrient soils of the CFR and Western Australia (Brundrett & Abbott 1991). Members of families such as the Aizoaceae and Mesembryanthemaceae, which are commonly found associated with disturbed areas in the CFR, are non-mycorrhizal when growing in undisturbed ecosystems. This supports the report that at the ecosystem level, patterns of mycorrhizal and non-mycorrhizal species among weedy species followed taxonomic divisions irrespective of growth form (Pendleton & Smith 1983). As most of the data here are obtained from plants growing in the field and mycorrhizal status was usually consistent at the family level, generalizations can be made regarding the mycorrhizal status of the Cape Flora, provided cognisance is taken that exceptions may arise. The mycorrhizal status of the flora of the three study sites, representing three lowland vegetation types is summarized in Table 1. If the mycorrhizal status of species listed in Bond & Goldblatt (1984) is inferred from that of taxonomically related species which have been examined, we conclude that 62% of the flora form VAM,

TABLE 1. — Summary of the mycorrhizal status of the vegetation growing in Sand Plain Lowland Fynbos, Renosterveld and Strandveld communities, and the Cape Floristic Region (CFR)

	VAM (%)	ABS (%)	ERIC (%)	ORCH (%)	Unknown (%)
Lowland Fynbos	72	23	<1	1–2	3
Renosterveld	77	18	0	?	5
Strandveld	64	27	0	?	9
CFR	62	23	8	2	4

VAM = vesicular-arbuscular mycorrhizal; ABS = non-mycorrhizal; ERIC = ericoid mycorrhizal; ORCH = orchid mycorrhizal.

plants without mycorrhizas are the next largest group, ericoid and orchid mycorrhizas are found in less than 10% of the flora, and the mycorrhizal status of 4% of the flora is unknown (Table 1).

The proportion of non-mycorrhizal species in the CFR is high when compared to many other vegetation types worldwide (Brundrett 1991). As non-mycorrhizal plants are normally associated with high levels of disturbance, or edaphically and climatically extreme conditions, the non-mycorrhizal flora in the CFR is atypical in that representatives of two families that dominate the vegetation of the CFR, the Proteaceae and Restionaceae, are non-mycorrhizal. The evolutionary and ecological significance of this needs further exploration. The diversity of mycorrhizal types is possibly an indication that no one type of mycorrhiza or other nutrient acquiring adaptation is pre-eminently suited to the environmental conditions in the CFR and that the diversity of nutrient acquisition mechanisms in the CFR has probably promoted species co-existence.

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APPENDIX -A preliminary list of the mycorrhizal status of plants occurring in the Cape Floristic Region

	No.	Loc.	Lit.	Myc.	Notes
MAGNOLIOPSIDA					
MAGNOLIIDAE					
LAURACEAE					
<i>Ocotea bullata</i> (Burch.) Baill.			EML	ENDO	
FUMARIACEAE					
<i>Cysticapnos vesicarius</i> (L.) Fedde	13	N	B, M & A	ABS	
CARYOPHYLLIDAE					
AIZOACEAE					
<i>Aizoon sarmentosum</i> L. f.	1	H	A & S	ABS	
<i>Galenia africana</i> L.	5	N	B, M & A	ABS	
<i>Limeum aethiopicum</i> Burm.	1	P	A & S	ABS	
Pharnaceum					
sp. cf. <i>P. croceum</i> E. Mey. ex Fenzl	2	P	A & S	ABS	
<i>incanum</i> L.	4	P	A & S	ABS	Vesicles, other fungi may be present
<i>scleranthoides</i> Sond.	1	P	A & S	ABS	
sp.	3	N	B, M & A	ABS	
<i>Polypoda capensis</i> Presl	3	P	A & S	ABS	Vesicles may be present
Tetragonia					
<i>fruticosa</i> L.	7	N	B, M & A	ABS	
<i>portulacoides</i> Fenzl	2	P	A & S	ABS	
MESEMBRYANTHEACEAE					
<i>Carpanthea pomeridiana</i> (L.) N.E. Br.	2	PH	A & S	ABS	Other fungi present
Carpobrotus					
<i>acinaciformis</i> (L.) L. Bol.	1	M	A & S	ABS	<i>Olpidium</i> , DSH, other fungi present
<i>edulis</i> (L.) L. Bol.	3	P	A & S	ABS	Arbuscules in one specimen, vesicles and other fungi present
<i>Dorotheanthus bellidiformis</i> (Burm. f.) N.E. Br.	3	P	A & S	ABS	DSH, other fungi present
Drosanthemum					
<i>floribundum</i> (Haw.) Schwant.	5	N	B, M & A	ABS	
sp.	4	N	B, M & A	ABS	
<i>Jordaaniella dubia</i> (Haw.) H.E.K. Hartm.	1	M	A & S	ABS	
Lampranthus					
<i>aurantiacus</i> (DC.) Schwant.	2	P	A & S	ABS	Other fungi present
sp.	1	H	A & S	ABS	
<i>Mesembryanthemum</i> sp.	16	N	B, M & A	ABS	
Ruschia					
<i>macowanii</i> (L. Bol.) Schwant.	3	M	A & S	ABS	Vesicles, DSH, other fungi present
sp.	2	N	B, M & A	ABS	
CHENOPODIACEAE					
Atriplex					
<i>halimus</i> L.*	2	N	B, M & A	ABS	
<i>nummularia</i> Lindl.*	2	N	B, M & A	ABS	
<i>semibaccata</i> R. Br.*	5	N	B, M & A	VAM	
<i>lindleyi</i> Moq.*	23	N	B, M & A	ABS	
<i>Chenopodium murale</i> L.*	11	N	B, M & A	ABS	
<i>Exomis</i> sp.	27	N	B, M & A	ABS	
<i>Manochlamys albicans</i> (Ait.) Aell.	1	N	B, M & A	ABS	
ILLECEBRACEAE					
Silene					
<i>clandestina</i> Jacq.	2	P	A & S	ABS	Other fungi present
<i>undulata</i> Ait.	2	M	A & S	ABS	Vesicles, DSH, other fungi present
sp. 1	2	H	A & S	ABS	Arbuscules in one specimen, other fungi present
sp. 2	1	N	B, M & A	ABS	
POLYGONACEAE					
<i>Emex australis</i> Steinh.*	12	N	B, M & A	ABS	
<i>Rumex cordatus</i> Poir.	4	P	A & S	ABS	Vesicles, DSH, other fungi present
PLUMBAGINACEAE					
<i>Limonium perigrinum</i> (Berg.) R.A. Dyer	2	M	A & S	ABS	Needs confirmation, small root samples

* introduced species.

No. = number of specimens examined.

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	No.	Loc.	Lit.	Myc.	Notes
DILLENIACEAE					
STERCULIACEAE					
<i>Hermannia</i>					
<i>alnifolia</i> L.	1	P	A & S	VAM	
<i>multiflora</i> Jacq.	4	P	A & S	VAM	
MALVACEAE					
<i>Lavatera trimestris</i> L.*	1	N	B, M & A	ABS	
BRASSICACEAE					
<i>Brassica</i> sp.*	2	N	B, M & A	ABS	
<i>Heliophila</i>					
<i>africana</i> (L.) <i>Marais</i>	1	M	A & S	ABS	
<i>arenaria</i> Sond.	1	P	A & S	ABS	
sp. 1	1	P	A & S	ABS	
sp. 2	1	M	A & S	ABS	
ERICACEAE					
<i>Erica</i>					
<i>bauera</i> Andr.			RKR	ERIC	
<i>blenna</i> Salisb.			RKR	ERIC	
<i>campanularis</i> Salisb.			RKR	ERIC	
<i>cerinthoides</i> L.			RKR	ERIC	
<i>clavispala</i> Guth. & Bol.		O	ABL	ERIC	
<i>daphniflora</i> Salisb.			RKR	ERIC	
<i>glaucia</i> Andr.		pot	A & S	ERIC	
<i>grandiflora</i> L. f.		pot	A & S	ERIC	
<i>gracilis</i> Wendl.		pot	A & S	ERIC	
<i>hispidula</i> L.		K	FC, S & M	ERIC	
<i>inflata</i> Thunb.			RKR	ERIC	
<i>lateralis</i> Willd.			RKR	ERIC	
<i>mammosa</i> L.			RKR	ERIC	
<i>mauritanica</i> L.			S & M	ERIC	
<i>perspicua</i> Wendl.			EML	?	Hair roots not examined
<i>regia</i> Bartling			RKR, A & S	ERIC	
<i>sessiliflora</i> L.			RKR	ERIC	
<i>ventricosa</i> Thunb.			RKR	ERIC	
<i>Grisebachia plumosa</i> Klotzsch	4	P	A & S	ERIC	
<i>Simocheilus depressus</i> (Licht.) Benth.		O	ABL	ERIC	
EBENACEAE					
<i>Diospyros glabra</i> (L.) De Winter	1	P	A & S	VAM	
PRIMULACEAE					
<i>Anagallis arvensis</i> L.*	3	M H	A & S	VAM	
ROSIDAE					
CUNONIACEAE					
<i>Cunonia capensis</i> L.			EML	ENDO	
<i>Platylophus trifoliatus</i> (L. f.) D. Don			EML	ENDO	
BRUNIACEAE					
<i>Staavia</i>					
<i>dodii</i> H. Bol.		O	AG	VAM	
<i>radiata</i> (L.) Dahl	4	P	A & S	VAM	
CRASSULACEAE					
<i>Cotyledon orbiculata</i> L.	2	M	A & S	ABS	Vesicles, <i>Olpidium</i> present
<i>Crassula</i>					
<i>capensis</i> (L.) Baill.	1	H	A & S	VAM	Needs confirmation
<i>dichotoma</i> L.	5	P M	A & S	ABS	Vesicles, <i>Olpidium</i> present
<i>expansa</i> Dryand.	2	N	B, M & A	ABS	
<i>filiformis</i> (Eckl. & Zeyh.) Dietr.	1	P	A & S	ABS	DSH present
<i>glomerata</i> Berg.	2	M	A & S	ABS	Other fungi present
<i>oblanceolata</i> Schönl. & Bak. f.	5	N	B, M & A	ABS	
<i>tomentosa</i> Thunb.	2	M	A & S	ABS	

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MONTINIACEAE					
<i>Montinia caryophyllacea</i> Thunb.	1	P	A & S	VAM	
ROSACEAE					
<i>Cliffortia</i>					
<i>ruscifolia</i> Weim.	1+	H B	A & S, ABL	VAM	ABL no VAM
<i>polygonifolia</i> L.	3	P	A & S	VAM	
<i>Grielum humifusum</i> Thunb.	2	N	B, M & A	VAM	
MIMOSACEAE					
<i>Acacia</i>					
<i>cyclops</i> A. Cunn ex G. Don*	25	P	A & S	VAM	Other fungi present
<i>karroo</i> Hayne		pot	A & S	VAM	
<i>saligna</i> (Labill.) Wendl.*	12+	P	A & S, H & M	VAM	VAM sometimes ABS, <i>Olpidium</i> , DSH, other fungi often present
FABACEAE					
<i>Amphithalia ericifolia</i> Eckl. & Zeyh.	1	P	A & S	VAM	
<i>Aspalathus</i>					
<i>albena</i> L.	2+	P	A & S	VAM	Infection slight (A & S), cluster roots present
<i>divaricata</i> Thunb.	1	P	A & S	ABS	Needs confirmation, other fungi present
<i>flexuosa</i> Thunb.	10	P	A & S, H & M	VAM	Other fungi present
<i>linearis</i> (Burm. f.) Dahlg.		pot	A & S	VAM	Cluster roots present
<i>spinescens</i> Thunb.	23	P	A & S	VAM	Cluster roots present, <i>Olpidium</i> , DSH, other fungi present
<i>ternata</i> (Thunb.) Druce	1	P	A & S	ABS	Needs confirmation
sp. 1	2	M	A & S	VAM	
sp. 2	1	H	A & S	VAM	
<i>Indigofera</i> sp.	3	M	A & S	VAM	
<i>Lotononis involucreta</i> Benth.	2	P	A & S	ABS	Needs confirmation
<i>Medicago</i>					
<i>polymorpha</i> L.*	2	M	A & S	VAM	
sp.*	6	N	B, M & A	VAM	
<i>Otholobium</i>					
<i>fruticans</i> (L.) C.H. Stirton		pot	A & S	VAM	
<i>hirtum</i> C.H. Stirton	8	P	A & S	VAM	
sp.	1	H	A & S	VAM	
<i>Podalyria</i>					
<i>calyptrata</i> Willd.		pot	A & S	VAM	
<i>cuneifolia</i> Vent.		pot	A & S	VAM	
<i>sericea</i> R. Br.	2	P	A & S	VAM	
<i>Priestleya</i>					
<i>glauca</i> Salter	2	H	A & S	VAM	
<i>sericea</i> (L.) E. Mey.	1	P	A & S	VAM	
<i>Psoralea pinnata</i> L.		pot	A & S	VAM	
<i>Rafnia angulata</i> Thunb.	2+	P	A & S, H & M	VAM	ABS in A & S
<i>Virgilia oroboides</i> (Berg.) Salter		pot	A & S, EML	VAM	EML reports absence of fungi
PROTEACEAE					
<i>Faurea macnaughtonii</i> Phil.	3		A & S, EML	ABS	EML reports ENDO, no fungi present in young roots, fungi with vesicles in dead roots
<i>Hakea sericea</i> Schrad.*		pot	A & S	ABS	
<i>Leucadendron laeureolum</i> (Lam.) Fourc.		pot	A & S	ABS	
<i>Leucospermum parile</i> (Salisb. ex Knight) Sweet	3	P	A & S	ABS	Other fungi present
<i>Protea</i>					
<i>burchellii</i> Stapf	1	P	A & S	ABS	Other fungi present
<i>scolymocephala</i> (L.) Reich.	2	P	A & S	ABS	Other fungi present
<i>Serruria fasciflora</i> Salisb. ex Knight	2	P	A & S	ABS	
PENAEACEAE					
<i>Stylapteris fruticosus</i> (L. f.) Juss.	3	P	A & S	VAM	
THYMELAEACEAE					
<i>Cryptadenia grandiflora</i> (L. f.) Meisn.	1+	P	A & S, M & R	VAM	
<i>Passerina paleacea</i> Wikstr.		pot	A & S	VAM	

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THYMELAEACEAE (cont.)					
<i>Passerina vulgaris</i> Thoday	3	P	A & S	VAM	
<i>Struthiola</i>					
sp. 1	2	P	A & S	VAM	
sp. 2	2	P	A & S	VAM	
CORNACEAE					
<i>Curtisia dentata</i> (Burm. f.) C.A. Sm.			EML	ENDO	
SANTALACEAE					
<i>Thesium</i>					
<i>densiflorum</i> A. DC.	2	P	A & S	ABS	Other fungi present
sp. cf. <i>T. strictum</i> Berg.	1	P	A & S	ABS	
sp. 1	1	P	A & S	ABS	Other fungi present
sp. 2	1	P	A & S	ABS	DSH, other fungi present
CELASTRACEAE					
<i>Putterlickia pyracantha</i> (L.) Szyszyl.	1	M	A & S	VAM	
ICACINACEAE					
<i>Apodytes dimidiata</i> E. Mey. ex Arn.			EML	ENDO	
EUPHORBIACEAE					
<i>Clutia</i>					
<i>alaternoides</i> L.	2	P	A & S	VAM	
<i>daphnoides</i> Lam.	1	M	A & S	VAM	
sp. 1	1	P	A & S	VAM	
sp. 2	1	H	A & S	VAM	
<i>Euphorbia</i>					
<i>burmannii</i> E. Mey. ex Boiss.	2	M	A & S	VAM	
<i>peplus</i> L.*	2	M H	A & S	VAM	
RHAMNACEAE					
<i>Phylla</i>					
<i>cephalantha</i> Sond.	1	P	A & S, M & R	VAM	Confirmed in pot experiments
<i>ericoides</i> L.	5	P	A & S	VAM	
<i>plumosa</i> L.	1	P	A & S	VAM	
<i>stipularis</i> L.	5	P	A & S, M & R	VAM	
sp. cf. <i>P. rubra</i> Willd.	1	M	A & S	VAM	
POLYGALACEAE					
<i>Muraltia</i>					
<i>decipiens</i> Schltr.	1	H	A & S	VAM	
<i>dumosa</i> (Poir.) DC.	5	P	A & S	VAM	
<i>thunbergii</i> Eckl. & Zeyh.	1	P	A & S	VAM	
<i>Polygala</i>					
<i>affinis</i> DC.	3	H	A & S	VAM	Fine endophyte in one
<i>garcinii</i> DC.	3	P	A & S	VAM	
<i>virgata</i> Thunb.		pot	A & S	VAM	
ANACARDIACEAE					
<i>Rhus rosmarinifolia</i> Vahl	1	P	A & S	VAM	DSH present
RUTACEAE					
<i>Agathosma</i>					
<i>capensis</i> (L.) Duemmer	2	H	A & S	VAM	
<i>collina</i> Eckl. & Zeyh.		pot	A & S	VAM	
<i>gonaquensis</i> Eckl. & Zeyh.		pot	A & S	VAM	
<i>imbricata</i> (L.) Willd.	6	P	A & S	VAM	Other fungi present
<i>ovata</i> (Thunb.) Pillans		pot	A & S	VAM	
ZYGOPHYLLACEAE					
<i>Zygophyllum</i>					
<i>flexuosum</i> Eckl. & Zeyh.	2	M	A & S	ABS	
<i>morgsana</i> L.	14	N	B, M & A	ABS	
<i>sessilifolium</i> L.	1	P	A & S	ABS	
<i>spinosum</i> L.	2	P	A & S	ABS	DSH, vesicles present

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OXALIDACEAE					
Oxalis					
capillacea <i>E. Mey. ex Sond.</i>	1	P	A & S	VAM	
luteola <i>Jacq.</i>	3	P	A & S	VAM	
sp. cf. <i>O. tenuifolia Jacq.</i>	1	H	A & S	VAM	
obtusata <i>Jacq.</i>	6	PMN	A & S, B, M & A	VAM	Fine endophyte, DSH present
pes-caprae <i>L.</i>	11	PMN	A & S, B, M & A	VAM	
polyphylla <i>Jacq.</i>	1	P	A & S	VAM	
purpurea <i>L.</i>	1	P	A & S	VAM	
tomentosa <i>L. f.</i>	1	H	A & S	VAM	
sp. 1	1	B	ABL	ABS	
sp. 2	2	N	B, M & A	VAM	
GERANIACEAE					
<i>Erodium incarnatum (L.) L'Hérit.</i>	1	H	A & S	VAM	Other fungi present
<i>Monsonia speciosa L. f.</i>	1	H	A & S	VAM	
Pelargonium					
elongatum (<i>Cav.</i>) <i>Salisb.</i>	1	H	A & S	VAM	
ovale (<i>Burm. f.</i>) <i>L'Hérit.</i>	3	P	A & S	VAM	
senecioides <i>L'Hérit.</i>	2	M	A & S	VAM	
triste (<i>L.</i>) <i>L'Hérit.</i>	3	P	A & S	VAM	DSH, other fungi present
sp. 1	1	P	A & S	VAM	
sp. 2	2	M	A & S	VAM	
APIACEAE					
Annesorrhiza					
sp. cf. <i>A. capensis Cham. & Schlecht.</i>	1	P	A & S	VAM	
sp.	1	H	A & S	VAM	
<i>Chamarea capensis (Thunb.) Eckl. & Zeyh.</i>	2	H	A & S	VAM	
<i>Torilis arvensis (Huds.) Link</i>	2	M	A & S	VAM	
ASTERIDAE					
GENTIANACEAE					
<i>Orphium frutescens (L.) E. Mey.</i>	1	M	A & S	VAM	Morphology of both spp.
<i>Sebaea exacoides (L.) Schinz</i>	3	P J	A & S	VAM	Typical of Gentianaceae VAM
APOCYNACEAE					
<i>Gonioma capensis L.</i>			EML	ENDO	
ASCLEPIADACEAE					
<i>Microlooma tenuifolium K. Schum.</i>	1	H	A & S	VAM	
<i>Secamone alpinii Schultes</i>	2	M	A & S	VAM	
SOLANACEAE					
Solanum					
americanum <i>Mill.*</i>	2	N	B, M & A	VAM	
guineense <i>L.</i>	1	H	A & S	VAM	
BORAGINACEAE					
<i>Lobostemon fruticosus (L.) Buek</i>	2	P	A & S	VAM	Other fungi present
LAMIACEAE					
<i>Ballota africana (L.) Benth.</i>	2	M H	A & S	VAM	ABS in one
Salvia					
africana-caerulea <i>L.</i>	2	P H	A & S	VAM	ABS in one, other fungi present
chamaeagnea <i>Berg.</i>	1	H	A & S	VAM	
lanceolata <i>Lam.</i>	4	P M	A & S	VAM	<i>Olpidium</i> , other fungi present
OLEACEAE					
<i>Olea capensis L.</i>			EML	ENDO	
SCROPHULARIACEAE					
<i>Diascia diffusa Benth.</i>	4	P	A & S	VAM	<i>Olpidium</i> , other fungi present
<i>Manulea tomentosa (L.) L.</i>	3	M	A & S	ABS	Or very slight VAM, <i>Olpidium</i> , other fungi present

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SCROPHULARIACEAE (cont.)					
Nemesia					
<i>affinis Benth.</i>	7	P H	A & S	VAM	ABS in some, <i>Olpidium</i> , other fungi present
<i>versicolor E. Mey. ex Benth.</i>	12	PMN	A & S, B, M & A	VAM	ABS in many at P and M, <i>Olpidium</i> , other fungi present
<i>barbata (Thunb.) Benth.</i>	1	H	A & S	VAM	
<i>Phyllopodium heterophyllum (L. f.) Benth.</i>	2	P	A & S	ABS	Or very slight VAM, other fungi present
Polycarena					
<i>capensis (L.) Benth.</i>	5	P	A & S	ABS	Or very slight VAM, <i>Olpidium</i> , other fungi present
<i>cephalophora (Thunb.) Levyns</i>	3	P	A & S	ABS	
<i>Sutera linifolia (Thunb.) Kuntze</i>	1	H	A & S	VAM	Other fungi present
Zaluzianskya					
<i>divaricata Walp.</i>	1	P	A & S	VAM	Slight VAM infection
<i>villosa (Thunb.) F.W. Schmidt</i>	5	M	A & S	ABS	<i>Olpidium</i> , other fungi present
sp.	4	N	B, M & A	ABS	
SELAGINACEAE					
<i>Dischisma capitatum (Thunb.) Croisy</i>	1	H	A & S	ABS	DSH, other fungi present
Hebenstretia					
<i>dentata L.</i>	1	M	A & S	ABS	<i>Olpidium</i> , other fungi present
<i>repens Jarosz</i>	1	P	A & S	VAM	Slight VAM infection
CAMPANULACEAE					
Microcodon					
<i>glomeratum A. DC.</i>	3	M	A & S	VAM	<i>Olpidium</i> present
<i>hispidulum (Thunb.) Sond.</i>	1	H	A & S	VAM	Slight VAM infection, fine endophyte present
<i>Roella ciliata L.</i>	2	P	A & S	VAM	
<i>Wahlenbergia capensis (L.) A. DC.</i>	2	H	A & S	VAM	
LOBELIACEAE					
<i>Cyphia digitata (Thunb.) Willd.</i>	3	M H	A & S	VAM	
<i>Lobelia coronopifolia L.</i>	4	P	A & S	VAM	Fine endophyte
RUBIACEAE					
Anthospermum					
<i>aethiopicum L.</i>	9+	PMHB	A & S, ABL	VAM	
sp. 1	1	H	A & S	VAM	
<i>Galium tomentosum Thunb.</i>	2	N	B, M & A	ABS	
ASTERACEAE					
<i>Arctotheca calendula (L.) Levyns</i>	10	M N	A & S, B, M & A	VAM	<i>Olpidium</i> , DSH, other fungi present
Arctotis					
<i>leptorhiza DC.</i>	1	P	A & S	VAM	
sp.	1	P	A & S	VAM	
<i>Athanasia trifurcata (L.) L.</i>	1	H	A & S	VAM	
<i>Cenia turbinata (L.) Pers.</i>	5	M H	A & S	VAM	
<i>Chrysanthemoides incana (Burm. f.) T. Norl.</i>	1	M	A & S	VAM	
<i>Chrysocoma ciliata L.</i>	1	H	A & S	VAM	
<i>Cineraria geifolia (L.) L.</i>	1	M	A & S	VAM	
<i>Cotula coronopifolia L.</i>	1	H	A & S	ABS	Needs confirmation
<i>Didelta spinosa (L. f.) Ait.</i>	2	N	A & S, B, M & A	VAM	
<i>Dimorphotheca pluvialis (L.) Moench</i>	8	P M H	A & S	VAM	Fine endophyte, <i>Olpidium</i> , other fungi present
Elytropappus					
<i>glandulosus Less.</i>	1	P	A & S	VAM	
<i>rhinocerotis (L. f.) Less.</i>	3	H	A & S	VAM	Other fungi present
Eriocephalus					
sp. 1	2	M	A & S	VAM	
sp. 2	4	H	A & S	VAM	
sp. 3	1	P	A & S	VAM	
<i>Felicia tenella (L.) Nees</i>	4	P M H	A & S	VAM	<i>Olpidium</i> , other fungi present
Gazania					
<i>ciliaris DC.</i>	4	P	A & S	VAM	
sp.	1	H	A & S	VAM	
<i>Gymnodiscus capillaris (L. f.) Less.</i>	4	P	A & S	VAM	ABS in some, <i>Olpidium</i> , other fungi present

* introduced species.

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APPENDIX—A preliminary list of the mycorrhizal status of plants occurring in the Cape Floristic Region (continued)

	No.	Loc.	Lit.	Myc.	Notes
ASTERACEAE (cont.)					
<i>Helichrysum</i>					
<i>cymosum</i> (L.) D. Don	1	P	A & S	VAM	
<i>indicum</i> (L.) Grierson	1	P	A & S	VAM	
<i>pandurifolium</i> Schrank	1	H	A & S	VAM	
<i>revolutum</i> (Thunb.) Less.	2	M H	A & S	VAM	
<i>teretifolium</i> (L.) D. Don	3	M H	A & S	VAM	<i>Olpidium</i> present
sp.	1	B	ABL	ENDO	
<i>Ifloga ambigua</i> (L.) Druce	5	P	A & S	VAM	
<i>Lachnospermum fasciculatum</i> (Thunb.) Baill.	2	P	A & S	VAM	
<i>Leysera gnaphalodes</i> (L.) L.	2	H	A & S	VAM	
<i>Matricaria tenella</i> DC.	20	N	B, M & A	VAM	
<i>Metalsia</i>					
<i>adunca</i> Less.	1	P	A & S	ABS	Needs confirmation
<i>muricata</i> (L.) D. Don	4+	P	A & S, M & R	VAM	ABS in some, other fungi present
<i>Oedera imbricata</i> Lam.	1	P	A & S	VAM	
<i>Osteospermum</i>					
<i>clandestinum</i> (Less.) T. Norl.	10	H N	A & S, B, M & A	VAM	
<i>spinosum</i> L.	1	H	A & S	VAM	
<i>Othonna</i>					
<i>bulbosa</i> L.	1	P	A & S	VAM	
<i>digitata</i> L.	4	P	A & S	VAM	Other fungi present
<i>filicaulis</i> Jacq.	2	H	A & S	VAM	<i>Olpidium</i> , other fungi present
<i>parviflora</i> Berg.	1	H	A & S	VAM	
<i>stenophylla</i> Levyns	3	P	A & S	VAM	
<i>Petalacte coronata</i> (L.) D. Don	6	P	A & S	VAM	Other fungi present
<i>Relhania squarrosa</i> (L.) L'Hérit.	1	H	A & S	VAM	<i>Olpidium</i> present
<i>Senecio</i>					
<i>arenarius</i> Thunb.	9	P M H	A & S	VAM	<i>Olpidium</i> , other fungi present
<i>burchellii</i> DC.	1	P	A & S	VAM	Other fungi present
<i>elegans</i> L.	1	M	A & S	VAM	
<i>repandus</i> Thunb.	1	H	A & S	VAM	
<i>Stoebe gomphrenoides</i> Berg.	2	P	A & S	VAM	Fine endophyte present
<i>Troglophytum parvulum</i> (Harv.) Hilliard & Burt	1	H	A & S	VAM	
<i>Ursinia anthemoides</i> (L.) Poir.	5	P M H	A & S	VAM	Other fungi present
LILIOPSIDA					
ARECIDAE					
ARACEAE					
<i>Zantedeschia aethiopica</i> (L.) Spreng.	2	M H	A & S	VAM	
COMMELINIDAE					
RESTIONACEAE					
<i>Cannamois parviflora</i> (Thunb.) Pillans	1	P	A & S	ABS	
<i>Hypodiscus willdenowia</i> (Nees) Mast.	1	P	A & S	ABS	
<i>Ischyrolepis monanthos</i> (Mast.) Linder	7	P	A & S	ABS	Other fungi present
<i>Staberoha distachya</i> (Roth.) Kunth	1	P	A & S	ABS	
<i>Thamnochortus punctatus</i> Pillans	2	P	A & S	ABS	
<i>Willdenowia</i>					
<i>arescens</i> Kunth	3	P	A & S	ABS	
<i>incurvata</i> (Thunb.) Linder	3	P	A & S	ABS	Other fungi present
CYPERACEAE					
<i>Ficinia</i> sp.	4	P M	A & S	ABS	Vesicles may be present
<i>Isolepis antarctica</i> Nees	1	P	A & S	ABS	Vesicles present
POACEAE					
<i>Aristida</i>					
sp. 1	2	P	A & S	ABS	<i>Olpidium</i> , other fungi present
sp. 2		B	ABL	ENDO	

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	No.	Loc.	Lit.	Myc.	Notes
POACEAE (cont.)					
Bromus					
pectinatus <i>Thunb.</i>	1	M	A & S	VAM	<i>Olpidium</i> , DSH, other fungi present
sp.	13	N	B, M & A	VAM	
Ehrharta					
calycina <i>J.E. Sm.</i>	10	P M N	A & S, B, M & A	VAM	VAM low at P and M, <i>Olpidium</i> , other fungi present
villosa <i>Schult. f.</i>					
sp.	2	P	A & S	ABS	<i>Olpidium</i> , other fungi present
Enneapogon sp.	3	P	A & S	VAM	Other fungi present
Enneapogon sp.	5	N	B, M & A	ABS	
Festuca scabra <i>Vahl</i>	1	P	A & S	VAM	
Lolium sp.	32	N	B, M & A	VAM	
Pentstemon angulatus (<i>Nees</i>) <i>Adamson</i>	3	M	A & S	VAM	VAM low, <i>Olpidium</i> , other fungi present
Stipagrostis zeyheri (<i>Nees</i>) <i>De Winter</i>	2	P	A & S	VAM	VAM ABS in one, other fungi present
Themeda triandra <i>Forssk.</i>		B	ABL	ENDO	
Tribolium uniolae (<i>L. f.</i>) <i>Renvoize</i>	1	P	A & S	VAM	VAM low, <i>Olpidium</i> , DSH, other fungi present
LILIIDAE					
HAEMODORACEAE					
Wachendorfia parviflora <i>W.F. Barker</i>	5	P	A & S	VAM	VAM ABS in some, DSH, other fungi present
AMARYLLIDACEAE					
Haemanthus					
pubescens <i>L. f.</i>	6	P	A & S	VAM	
sanguineus <i>Jacq.</i>	1	H	A & S	VAM	
ASPARAGACEAE					
Myrsiphyllum asparagoides (<i>L.</i>) <i>Willd.</i>	1	P	A & S	VAM	
Protasparagus					
capensis (<i>L.</i>) <i>Oberm.</i>	3	P	A & S	VAM	
exuvialis (<i>Burch.</i>) <i>Oberm.</i>	2	P	A & S	VAM	
ASPHODELACEAE					
Anthericum rangei <i>Engl. & Krause</i>	1	H	A & S	VAM	
Trachyantha					
chlamydephylla (<i>Bak.</i>) <i>Oberm.</i>	1	P	A & S	ABS	Needs confirmation
ciliata (<i>L. f.</i>) <i>Kunth</i>	2	M	A & S	VAM	DSH, other fungi present
hispida (<i>L.</i>) <i>Kunth</i>	2	P	A & S	VAM	
muricata (<i>L. f.</i>) <i>Kunth</i>	2	H	A & S	VAM	
tabularis (<i>Bak.</i>) <i>Oberm.</i>	4	P	A & S	VAM	
ERIOSPERMACEAE					
Eriospermum					
sp. 1	2	P	A & S	VAM	
sp. 2	1	N	B, M & A	VAM	
HYACINTHACEAE					
Albuca					
canadensis (<i>L.</i>) <i>Leighton</i>	5	P M N	A & S, B, M & A	VAM	Other fungi present
sp. cf. A. spiralis <i>L. f.</i>	2	P	A & S	VAM	
sp. cf. A. tenuifolia <i>Bak.</i>	1	P	A & S	VAM	
Lachenalia					
mutabilis <i>Sweet</i>	2	P	A & S	VAM	
sp. cf. L. rubida <i>Jacq.</i>	1	P	A & S	VAM	
Ornithogalum					
thyrsoides <i>Jacq.</i>	2	H	A & S	VAM	
suaveolens <i>Jacq.</i>	2	H	A & S	VAM	
HYPOXIDACEAE					
Spiloxene schlechteri (<i>H. Bol.</i>) <i>Garside</i>	1	H	A & S	VAM	
TECOPHILAEACEAE					
Cyanella hyacinthoides <i>L.</i>	1	H	A & S	VAM	

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	No.	Loc.	Lit.	Myc.	Notes
IRIDACEAE					
<i>Antholyza ringens</i> L.	1	P	A & S	VAM	DSH, other fungi present
<i>Aristea dichotoma</i> (Thunb.) Ker-Gawl.	1	P H	A & S	VAM	Intracellular hyphal coils
<i>Babiana</i>					
<i>ambigua</i> (Roem. & Schult.) G.J. Lewis	2	P	A & S	ABS	Needs confirmation, other fungi present
sp. cf. <i>B. nana</i> (Andr.) Spreng.	1	M	A & S	ABS	Needs confirmation, DSH, other fungi present
<i>tubulosa</i> (Burm. f.) Ker-Gawl.	1	M	A & S	VAM	
<i>Geissorrhiza</i> sp. cf. <i>G. aspera</i> Goldbl.	1	P	A & S	VAM	
<i>Gladiolus gracilis</i> Jacq.	1	P	A & S	ABS	Needs confirmation, other fungi present
<i>Homeria longistyla</i> Goldbl.	3	P	A & S	VAM	
<i>Lapeirousia anceps</i> (L. f.) Ker-Gawl.	4	P	A & S	VAM	
<i>Melasphaerula ramosa</i> (L.) N.E. Br.	1	H	A & S	VAM	
<i>Moraea</i>					
<i>angusta</i> (Thunb.) Ker-Gawl.	3	P	A & S	VAM	Other fungi present
<i>gawleri</i> Spreng.	1	H	A & S	VAM	
<i>Romulea schlechteri</i> Bég.	1	P	A & S	VAM	DSH, other fungi present
<i>Watsonia meriana</i> (L.) Mill.	2	P	A & S	VAM	
ORCHIDACEAE					
<i>Disa</i>					
<i>cornuta</i> (L.) Sw.	1	P	A & S	ORCH	
<i>uniflora</i> Berg.		pot	A & S	ORCH	
MISCELLANEOUS RECORDS					
CUPRESSACEAE					
<i>Widdringtonia nodiflora</i> (L.) Powrie		OK	ABL	ENDO	Unusual type
PODOCARPACEAE					
<i>Podocarpus falcatus</i> (Thunb.) R. Br. ex Mirb.	2	S	A & S	VAM	
ADIANTACEAE					
<i>Pellaea</i> sp.	1	H	A & S	ABS	

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Pollen morphology of *Curroria*, *Mondia*, *Socotranthus* and *Stomatostemma* (Periplocaceae)

R.L. VERHOEVEN* and H.J.T. VENTER*

Keywords: *Curroria*, *Mondia*, Periplocaceae, pollen morphology, *Socotranthus*, *Stomatostemma*

ABSTRACT

The pollen morphology of *Curroria* Planch., *Mondia* Skeels, *Socotranthus* Kuntze and *Stomatostemma* N.E. Br. was studied. All the genera are characterized by pollen grains arranged in tetrads. The arrangement of the grains may be rhomboidal, tetrahedral or decussate. The 4–6 pores present are restricted to the junction area of adjacent grains. The exine is smooth. Exine structure consists of an outer, homogeneous stratum (tectum) subtended by a granular stratum. The intine is well developed. The pollen grains of tetrads are connected by wall bridges (cross-wall cohesion). Except for small differences which may occur between species and genera in pollen size and arrangement of tetrads, the pollen is uniform in morphology.

UITTREKSEL

Die stuifmeelmorfologie van *Curroria* Planch., *Mondia* Skeels, *Socotranthus* Kuntze en *Stomatostemma* N.E.Br. is bestudeer. Al die genera word gekenmerk deur stuifmeelkorrels wat in tetraëde gerangskik is. Die rangskikking van die stuifmeelkorrels kan romboïdaal, tetraëdries of kruisgewys wees. Vier tot ses porieë kom voor en hulle is beperk tot die aansluitingsgebied tussen aangrensende stuifmeelkorrels. Die eksien is glad en bestaan uit 'n buitenste homogene stratum (tektum) en granulêre stratum daaronder. Die intien is goed ontwikkel. Die stuifmeelkorrels van tetraëde is verbind deur wandbrûe (dwarswandkohesie). Met die uitsondering van klein verskille tussen spesies en genera in stuifmeelgrootte en rangskikking van tetraëde, stem die stuifmeelkorrels in morfologie ooreen.

INTRODUCTION

Periplocaceae and Asclepiadaceae are two closely allied families with several features in common. The former was a subfamily (Periplocoideae) of the latter, but raised to family status by Schlechter (1924), a concept followed by Bullock (1957), a well known expert in this group. The Periplocaceae is related to the Apocynaceae on the one hand and to the Asclepiadaceae on the other. All three families have in common a milky latex, flowers with coronas, fruits composed of paired follicles and seeds with comas of hairs. The Periplocaceae is distinguished by its spatulate pollen carriers and pollen grains united in tetrads. This contrasts with single-grained pollen and absence of pollen carriers in the Apocynaceae, and pollinia attached to wishbone-shaped translators in the Asclepiadaceae.

Of the 50 genera included in the Periplocaceae, approximately 20 occur in Africa. Among these *Raphionacme* Harv. is the largest with 35 species endemic to Africa (Verhoeven & Venter 1988) and one endemic to Arabia (Miller & Biagi 1988). *Raphionacme* is also the only herbaceous genus, although a number of its species are climbers. Most of the other genera are lianous and a small number are shrubs.

Little information is available on the pollen morphology of the Periplocaceae. Schill & Jäkel (1978) investigated representatives of the following Periplocaceae in their study on the pollinaria of the Asclepiadaceae: *Cryptostegia* R. Br., *Ectadiopsis* Benth., *Hemidesmus* R. Br., *Omphalogonus* Baill., *Parquetina* Baill., *Periploca* L.,

Raphionacme, *Tacazzea* Decne. and *Zygostelma* Benth. Data on tetrad size and number of pores for nine collections of *Raphionacme*, three species of *Periploca*, two species of *Tacazzea*, and one species of *Cryptostegia*, *Ectadiopsis*, *Hemidesmus*, *Omphalogonus*, *Parquetina* and *Zygostelma* are also given. Lebrun *et al.* (1984) in their identification of *Raphionacme bingeri* (A. Chev.) Lebrun & Stork, give SEM results on seven *Raphionacme* species. Verhoeven & Venter (1988) have examined the pollen of 35 *Raphionacme* species; Verhoeven *et al.* (1989), five *Tacazzea* species and the monotypic genus *Petopentia* Bullock; and Venter *et al.* (1990) three species of *Ectadium* E. Mey.

In the present study pollen of *Curroria* Planch., *Mondia* Skeels, *Stomatostemma* N.E. Br. and *Socotranthus* Kuntze was examined with special reference to taxonomy. This paper thus constitutes part of a comprehensive palynological investigation and taxonomic revision of the African taxa of the Periplocaceae currently being undertaken by the authors.

Taxonomic aspects and distribution of genera

Curroria comprises five species. *C. decidua* Planch. is divided into three subspecies (Bullock 1953). With the exception of *C. decidua* subsp. *decidua* which occurs in southwestern Africa (Angola, Namibia and South Africa), all the other *Curroria* species and subspecies occur in the desert areas of east and northeast Africa (Tanzania, Kenya, Somalia, Ethiopia, with outlying stations in the Hadramawt and Socotra) (Bullock 1953). *Curroria* species are robust, erect shrubs or scramblers. The linear to spatulate leaves are borne in clusters on short shoots and opposite on long shoots. The petiole is absent or very short. Flowers are solitary or occur as few-flowered cymes in the axils of the leaves.

* Department of Botany and Genetics, University of the Orange Free State, P.O. Box 339, Bloemfontein 9300.
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Socotranthus is a monotypic genus. *S. socotranus* (Balf. f.) Bullock is found on the island of Socotra (Suqutra) east of the coast of Somalia. This is a large woody shrub of arid habitats. Its suborbicular leaves are opposite and the white flowers are grouped together in terminal cymes.

Mondia has two species, *M. ecornuta* (N.E. Br.) Bullock and *M. whitei* (Hook. f.) Skeels. Both species are lianas of moist forest in tropical and subtropical regions of Africa. They both bear large, cordate leaves and many-flowered axillary cymes. The flowers are showy, ranging from yellowish to reddish in colour.

Stomatostemma also comprises two species, *S. monteiroae* (Oliv.) N.E. Br. and *S. pendulina* Venter & D.V. Field. The first species is a climber with ovate leaves and large cymes of whitish-purple flowers, whereas the latter is a virgate shrub with linear leaves and large cymes of white flowers. Both species occur in dry forest.

MATERIAL AND METHODS

Pollen was obtained from herbarium specimens. For light microscopy (LM) pollen was acetolysed according to the method of Erdtman (1960), mounted in glycerine jelly and sealed with paraffin wax. Samples were examined with a Zeiss Photomicroscope. Measurements of tetrad size are based on a minimum of 15 tetrads per specimen. For scanning electron microscopy (SEM), pollen was

acetolysed, air-dried on stubs, coated with gold and examined with a Jeol Winsem 6400 microscope. For transmission electron microscopy (TEM) fresh material was used. Pollen carriers were fixed in 3% phosphate-buffered glutaraldehyde, postfixed in 1% osmium tetroxide, dehydrated in ethyl alcohol and embedded in Spurr's low-viscosity resin. Sections were cut with a glass knife, stained with uranyl acetate, followed by lead citrate, and examined with a Philips 300 electron microscope at 60 kV.

Pollen specimens examined

Curroria brevifolia Balf. f., no material available.

C. decidua subsp. *decidua* Planch., Warmbad, Namibia, Mar. 1986, Beukes 22 (BLFU); Mariental, Namibia, Sept.-Mar. 1959, Werdermann & Oberdieck 2261 (K); Usakos, Namibia, Feb. 1969, Jensen 93 (WIND); Ruacana Falls, Namibia, De Winter & Giess 7105 (WIND).

C. decidua subsp. *gillettii* (Hutch. & Bruce) Bullock, no material available.

C. decidua subsp. *volubilis* (Balf. f.) Bullock, Kishen, Socotra, Aug. 1956, Gwynne 96 (BM).

C. macrophylla A.R. Smith, Abd al Kuri, Somalia, Oct. 1966, Virzo A27 (K).

C. migiurtina (Chiov.) Bullock, no locality, no date, Collette 198 (K); Eil, Somalia, Nov. 1986, Lavranos & Carter et al. 24945 (K).

C. volubilis (Schltr.) Bullock, Yaida, Tanzania, Jan. 1970, Richards 25306 (K); Harrar, Ethiopia, Nov. 1970, De Wilde 7279 (WAG); Nyambiti, Tanzania, Mar. 1953, Tanner 1274 (BR).

Mondia ecornuta (N.E. Br.) Bullock, Pangani District, Tanzania, May 1950, Faulkner 558 (K); Kilifi District, Kenya, June 1973, Musyoki & Hansen 956 (K); Monyondzi, Congo, Nov. 1964, Bouquet 631 (P).

TABLE 1.—Diameter of pollen tetrads (μm)

Taxon		Tetrahedral	Rhomboidal
<i>Curroria</i>			
<i>brevifolia</i>	—	—	—
<i>decidua</i>			
subsp. <i>decidua</i>	1	32.5 (30–34) \pm 1.3 \times 31.3 (30–33) \pm 1.6	38 \times 28
	2	32.9 (30–36) \pm 1.4 \times 30.4 (27–34) \pm 2.1	34 \times 30
	3	32.0 (30–34) \pm 1.4 \times 30.9 (27–33) \pm 1.8	
	4	33.0 (30–36) \pm 1.2 \times 31.9 (30–33) \pm 0.9	
subsp. <i>gillettii</i>	—	—	—
subsp. <i>volubilis</i>	1	32.8 (30–36) \pm 2.3 \times 25.5 (24–28) \pm 1.0	36 \times 24
<i>macrophylla</i>	1	29.4 (27–35) \pm 3.1 \times 22.5 (22–24) \pm 1.1	36 \times 24
<i>migiurtina</i>	1	36.0 (31–41) \pm 2.8 \times 26.4 (22–28) \pm 2.1	41 \times 26
	2	33.9 (31–36) \pm 1.6 \times 25.3 (23–27) \pm 1.2	41 \times 24
<i>volubilis</i>	1	37.5 (29–42) \pm 4.0 \times 29.0 (27–32) \pm 1.6	44.5 (39–50) \pm 2.9 \times 28.5 (24–33) \pm 2.0
	2		46.3 (38–54) \pm 4.2 \times 28.5 (26–32) \pm 1.9
	3		48.5 (45–55) \pm 2.8 \times 27.5 (25–32) \pm 1.3
<i>Mondia</i>			
<i>ecornuta</i>	1	43.3 (41–46) \pm 1.7 \times 40.9 (38–42) \pm 1.4	53.3 (48–60) \pm 4.2 \times 46.7 (41–58) \pm 4.4
	2	43.9 (41–49) \pm 2.3 \times 39.6 (36–45) \pm 2.8	56 \times 42
	3	45 \times 42	57.3 (49–67) \pm 4.0 \times 44.6 (38–54) \pm 5.0
<i>whitei</i>	1	42.8 (39–45) \pm 2.1 \times 40.4 (36–44) \pm 3.2	
	2	41.4 (39–46) \pm 1.9 \times 40.0 (39–41) \pm 0.7	
<i>Socotranthus</i>			
<i>socotranus</i>	1	33.3 (28–36) \pm 2.9 \times 24.9 (22–27) \pm 1.8	
<i>Stomatostemma</i>			
<i>monteiroae</i>	1	52.7 (50–58) \pm 2.3 \times 51.5 (49–54) \pm 1.8	61 \times 51
	2	47.8 (45–50) \pm 1.5 \times 46.4 (43–50) \pm 1.8	55 \times 43
	3	44.7 (42–48) \pm 1.4 \times 42.2 (39–45) \pm 2.1	53 \times 39
<i>pendulina</i>	1	31.6 (29–35) \pm 1.9 \times 29.5 (27–32) \pm 1.4	39 \times 28

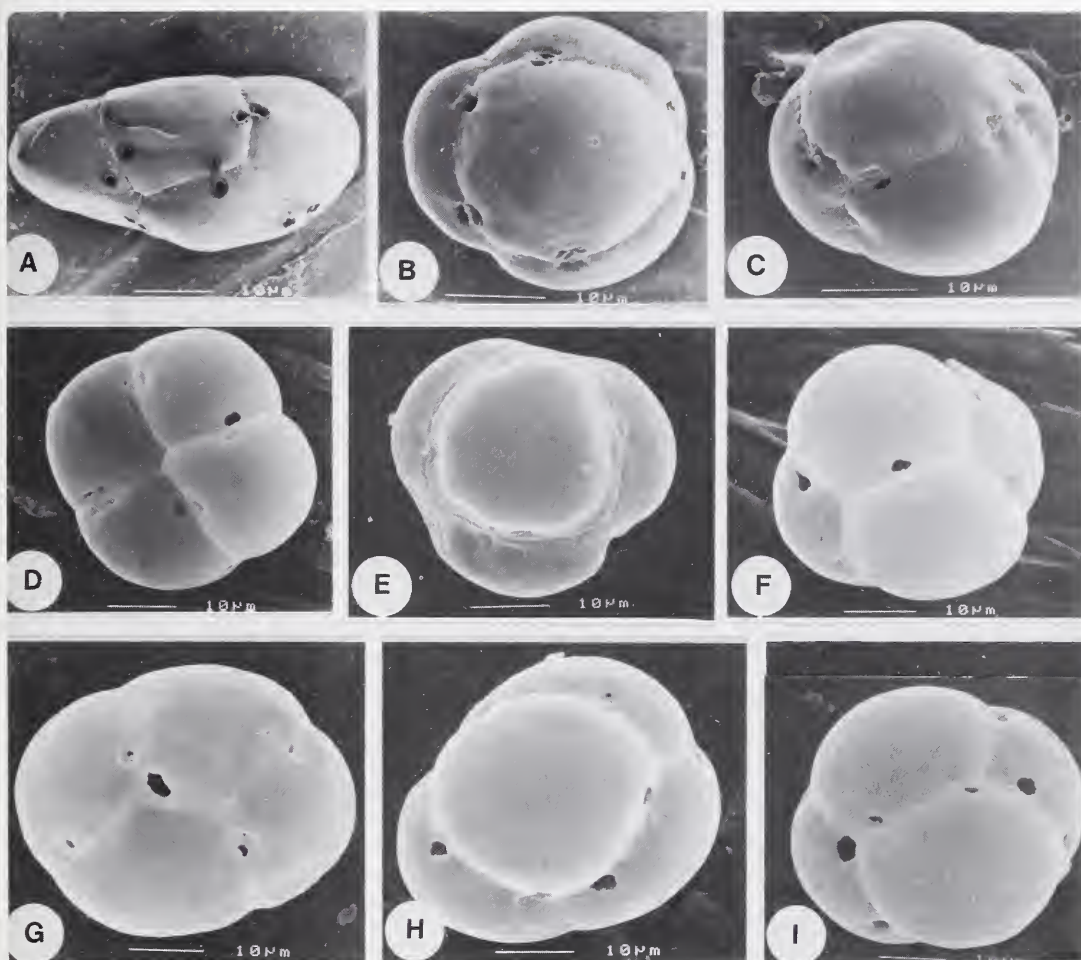


FIGURE 1.—SEM of tetrads of species. A, *Curroria volubilis*, Richards 25306 (K), rhomboidal tetrad. B, C, *C. decidua* subsp. *decidua*; B, tetrahedral tetrad, *De Winter & Giess* 7105 (WIND); C, decussate tetrad, *Beukes* 22 (BLFU). D–F, *Mondia whitei*: D, rhomboidal tetrad, *Venter* 9068 (BLFU); E, tetrahedral tetrad, *Scheepers* 1058 (PRU); F, decussate tetrad, *Venter* 9068 (BLFU). G–I, *Stomatostemma monteiroae*, *Pooley* 293 (NU): G, rhomboidal tetrad; H, tetrahedral tetrad; I, decussate tetrad. Scale bars = 10 µm.

M. whitei (Hook. f.) Skeels, Duiwelskloof, South Africa, Nov. 1960, *Scheepers* 1058 (PRU); Bloemfontein (glasshouse), South Africa, Dec. 1984, *Venter* 9068 (BLFU).

Socotranthus socotranus (Balf. f.) Bullock, Aola, Socotra, Mar. 1953, *Popov* 275 (BM).

Stomatostemma monteiroae (Oliv.) N.E. Br., Josini, South Africa, Nov. 1983, *Venter* 8988 (BLFU); Umfolozi Game Reserve, South Africa, Dec. 1961, *Ward* 3921 (PRE); Ndumu Game Reserve, South Africa, Dec. 1968, *Pooley* 293 (NU).

S. pendulina Venter & D.V. Field, Namina, Mozambique, July 1962, *Leach & Schelpe* 11441 (K).

RESULTS

Pollen morphology

The pollen grains in the four genera are united in tetrads, with the grains arranged rhomboidally (Figures 1A, D, G; 2A, D, G), tetrahedrally (Figures 1B, E, H; 2B, E, H) or decussately (Figures 1C, F, I; 2C, F, I; 3). The number of pores of individual grains of the tetrads may vary, but the morphology and position are the same for all the genera investigated. The pores are round, oval or irregular and

are restricted to the junction area of adjacent grains. Pores are sometimes covered with a thin layer of exine material.

Curroria

Pollen grains are arranged rhomboidally (Figures 1A; 2A), tetrahedrally (Figures 1B; 2B) or decussately (Figures 1C; 2C). In *C. volubilis* (Schltr.) Bullock the most common arrangement is rhomboidal, whereas in the other species it is tetrahedral and decussate. Size of tetrads varies from $27\text{--}42 \times 22\text{--}34 \mu\text{m}$ (tetrahedral) to $34\text{--}55 \times 24\text{--}33 \mu\text{m}$ (rhomboidal) (Table 1). Individual grains of tetrads have 4–6 pores.

Mondia

Pollen grains are arranged rhomboidally (Figures 1D; 2D), tetrahedrally (Figures 1E; 2E) or decussately (Figures 1F; 2F). Although rhomboidally arranged grains are present, the most common arrangements are tetrahedral and decussate. Size of tetrads varies from $39\text{--}49 \times 36\text{--}45 \mu\text{m}$ (tetrahedral) to $48\text{--}67 \times 38\text{--}58 \mu\text{m}$ (rhomboidal) (Table 1). Individual grains of the tetrads have 4–6 pores.

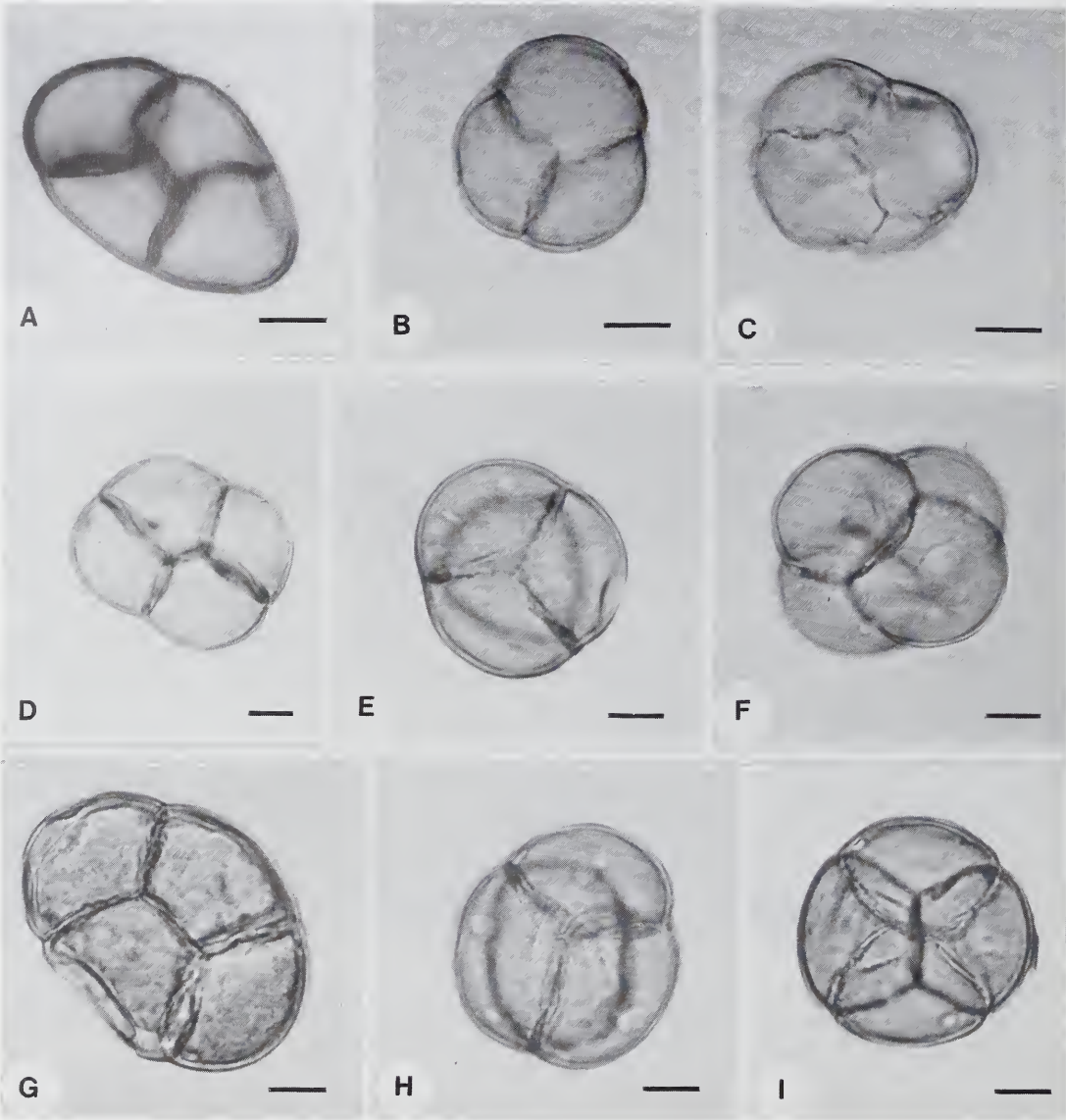


FIGURE 2.—LM photographs of tetrads of species. A, *Curroria volubilis*, Richards 25306 (K), rhomboidal tetrad. B, C, *C. decidua* subsp. *decidua*, Beukes 22 (BLFU): B, tetrahedral tetrad; C, decussate tetrad. D, E, *Mondia ecornuta*, Faulkner 558 (K): D, rhomboidal tetrad; E, tetrahedral tetrad. F, *M. whitei*, Venter 9068 (BLFU), decussate tetrad. G–I, *Stomatostemma monteiroae*: G, rhomboidal tetrad, Venter 8988 (BLFU); H, tetrahedral tetrad, Pooley 293 (NU); I, decussate tetrad, Pooley 293 (NU). Scale bars = 10 μ m.

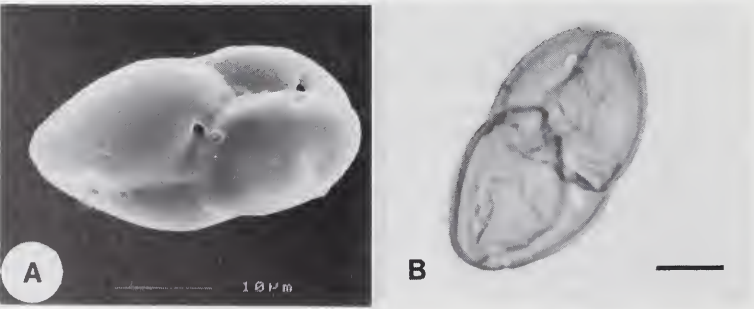


FIGURE 3.—Decussate tetrad of *Socotranthus socotranus*, Popov 275 (BM). A, SEM; B, LM photograph. Scale bars = 10 μ m.

Socotranthus

Pollen grains are arranged decussately (Figure 3) or tetrahedrally, very seldom rhomboidally. The decussate arrangement differs from that observed in other genera, in that the cells are arranged more parallel to each other and not perpendicular. Size of tetrads varies from $28\text{--}36 \times 22\text{--}27 \mu\text{m}$ (tetrahedral) (Table 1). Individual grains of the tetrads have 4–6 pores.

Stomatostemma

Pollen grains are arranged rhomboidally (Figures 1G; 2G), tetrahedrally (Figures 1H; 2H) or decussately (Figures 1I; 2I). The most common arrangements are tetrahedral and decussate. Size of tetrads varies from $29\text{--}58 \times 27\text{--}54 \mu\text{m}$ (tetrahedral) to $39\text{--}61 \times 28\text{--}51 \mu\text{m}$ (rhomboidal) (Table 1). Individual grains of the tetrads have 4–6 pores.

Exine structure

The exine is smooth and covered with a thin electron-dense layer (Figure 4A, arrow). Exine structure consists of an outer, homogeneous stratum (tectum) subtended by a granular stratum (Figure 4B). The tectum and granular stratum have the same electron density but the granular stratum has an irregular appearance because of channels which occur throughout it. The two layers are separated by a discontinuous line of osmiophilic substance. The fibrillar intine is well developed. The internal walls have the same structure as the exterior wall. Wall bridges consisting of intine and granular layer occur between adjacent grains (Figure 4C). The intine wall bridges indicate the position of pores in the internal wall of acetolysed pollen grains.

DISCUSSION

Compound pollen grains occur in more than 56 families of angiosperms (Erdtman 1945; Walker & Doyle 1975; Knox & McConchie 1986). The cohesion mechanisms in mature polyads were discussed by Knox & McConchie (1986). The cohesion of compound pollen occurs by attachment of the tectum (simple cohesion) or by connecting wall bridges (cross-wall cohesion). In cross-wall cohesion wall bridges are present in the common wall between adjacent grains, and these bridges comprise intine and granular layer in the Periplocaceae.

Pollen tetrads and polyads are common in a number of families and have been used in systematic treatments to separate genera and species (Oldfield 1959; Skvarla *et al.* 1975; Takahashi 1986). In the Mimosoideae extensive use of tetrads and polyads is made to separate genera (Guinet 1981a, b; Niezgoda *et al.* 1983). In the Periplocaceae, *Raphionacme* can be distinguished palynologically from the other genera by the 8–16 pores per pollen grain (Verhoeven & Venter 1988) as against 8–10 in *Baseonema* Schltr. & Rendle and 4–6 in the other genera. The monotypic *Petopentia natalensis* (Schltr.) Bullock can be distinguished from the other genera by the presence of linear and T-shaped tetrad arrangements (Verhoeven *et al.* 1989). In *Taczazzea*, *T. tomentosa* Bruce differs significantly from the other species by the width of the rhomboidal tetrads (Verhoeven *et al.* 1989).

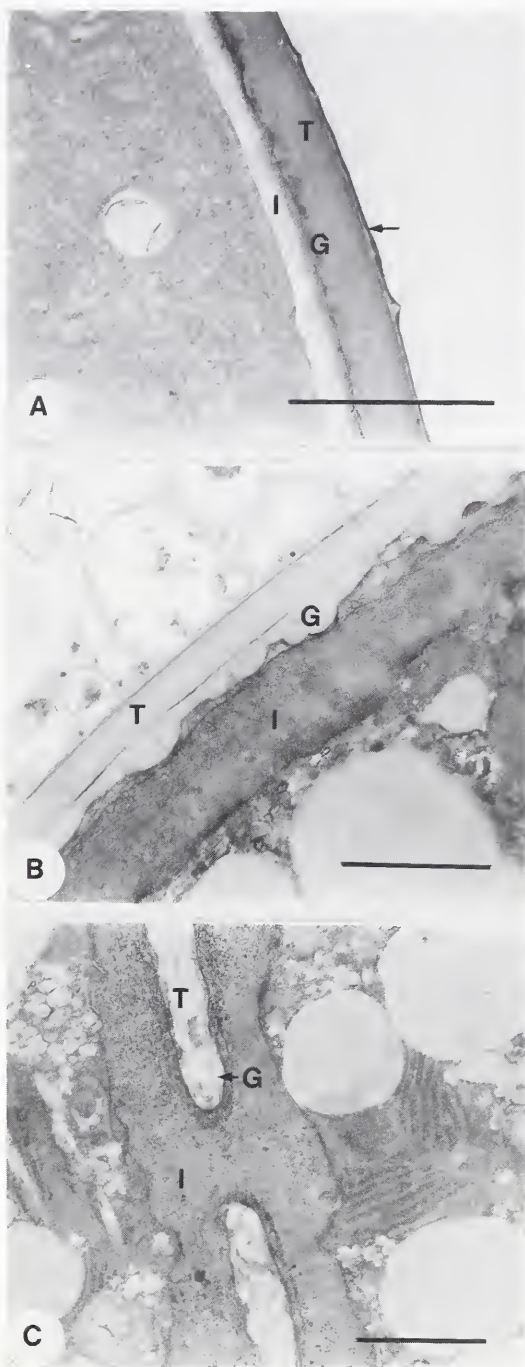


FIGURE 4.—A, B, TEM of pollen wall: A, *Curroria decidua* subsp. *decidua*, Beukes 22 (BLFU); B, *Mondia whitei*, Venter 9068 (BLFU). C, *M. whitei*, Venter 9068 (BLFU), internal wall. G, granular stratum; I, intine; T, tectum. Scale bars = $1 \mu\text{m}$.

The present study shows that *Stomatostemma pendulina* differs in tetrahedral size ($32 \times 30 \mu\text{m}$) from *S. monteiroae* ($48 \times 47 \mu\text{m}$). In *Curroria*, *C. volubilis* differs from the other species in that rhomboidal tetrad arrangement is predominant. *Socotranthus* can be identified by the unusual decussate arrangement of the tetrad.

The exine structure, consisting of a solid stratum (tectum) subtended by a granular stratum, appears to be without much variation in the representatives of the Periplocaceae studied thus far. The exine structure shows a resemblance with the general exine structure in the Apocynaceae. In the Apocynaceae the granular stratum is however, more variable, e.g. consisting of elements of unequal size and shape; subtended by a sole; larger granules towards the base and partly fused to a sole; faintly defined and delimited stratum with irregular voids containing traces of osmiophilic material (Nilsson 1986; 1990).

Although small differences may occur, the pollen morphology of the taxa investigated is rather uniform and thus of little value in the distinction of the species and genera investigated. The different, predominantly rhomboidal arrangement of the pollen tetrads of *Curroia volubilis* may indicate that this species should be placed in a different genus. It is significant that other floral characteristics show that *C. volubilis* does not belong in *Curroia* or to any of the genera investigated but to a new genus.

ACKNOWLEDGEMENTS

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Dynamics of the forest vegetation of the Umtiza Nature Reserve, East London

J.J. MIDGLEY* and P.N. GOBETZ**

Keywords: dynamics, eastern Cape, forests, grain, size-class distribution

ABSTRACT

The forest community at the Umtiza Nature Reserve near East London was surveyed using 24 plots (0.04 ha) in which all woody stems >0.5 m tall were enumerated. Based on a classification using numbers of stems of canopy species, it was assumed that basically only one forest community was sampled. Further multivariate analyses suggest that this forest is fine-grained. Sample plots were similarly placed in ordination space irrespective of whether woody species occurrence was used as importance value or if species occurrence per size class was used separately [seedlings (0.5–1.0 m), saplings (1–5 m) or canopy individuals (>5 m)]. An analysis of size-class distributions of the most common canopy species indicated that the majority of species exhibited inverse J-shaped size-class distributions. This is the expected pattern for a fine-grained forest. In these measures of dynamics, this forest is not fundamentally different to the more temperate Afromontane forests.

UITTREKSEL

'n Opname is gemaak van die woudgemeenskap in die Umtiza-natuurreservaat naby Oos-Londen; alle houtagtige stamme >0.5 m hoog is in aanmerking geneem. Gebaseer op 'n klassifikasie waarin aantal stamme van blaredakspesies gebruik word, is daar aangeneem dat basies slegs een woudgemeenskap ingesluit is. Verdere veelvoudige variantanalises dui daarop dat hierdie woud fyn gegrein is. Monsterpersele is eenders in ordinasieruimte geplaas ongeag of voorkoms van houtagtige spesies as belangrikheidswaarde gebruik is en of voorkoms van spesies per grootteklas afsonderlik gebruik is [saailinge (0.5–1.0 m), jong bome (1–5 m) of blaredak-individue (>5 m)]. Ontleding van grootteklas-verspreidings van die mees algemene blaredakspesies het getoon dat die meeste spesies omgekeerde J-vormige grootteklas-verspreidings vertoon het. Dit is die verwagte patroon vir 'n fyngegrin-woud. In hierdie metings van dinamika, verskil hierdie woud nie fundamenteel van die meer gematigde Afromontaanse woude nie.

INTRODUCTION

In brief, forest dynamics is the complex product of interactions between disturbance regime (e.g. type of disturbance, turnover rate), life histories of constituent species along a shade-tolerant to shade-intolerant continuum and particulars of the regeneration arena (e.g. regeneration bottlenecks due to biotic or abiotic events). As such the study of dynamics needs several inputs. In this preliminary study we concentrated on aspects of the grain and life history components of dynamics. By life histories we mean whether a species is relatively shade-tolerant 'climax' or shade-intolerant 'pioneer' and this we have inferred from size-class distributions.

By grain we mean 'the mosaic of structural phases' (Whitmore 1989); or the spatial patterns of seedlings/saplings and canopy individuals of the different species. Coarse-grained forests tend to have at least some (recently disturbed) areas which are dominated by shade-intolerant species. When plotted in ordination space, coarse-grained forests should show clear separation of plots according to whether pioneers or climax species are present, especially when their sizes are considered. In fine-grained forests most species can regenerate close to adults and therefore there are no great differences in species composition or size-class distributions amongst plots. In other words

the successional process occurs on a small spatial scale in fine-grained forests.

Recent work has shown that in many different forests at any one time gaps occupy about 1–2% of the area (Barden 1989; Connell 1989). In forests not subject to catastrophes these values suggest that stems in the small size classes of shade-intolerant species should be rare in comparison to the large bank of advance regeneration of shade-tolerant species. Thus the size-class distributions of shade-intolerant species should be flatter than those of shade-tolerant species. A forest comprised of many species with relatively flat size-class distributions should thus be a relatively coarse-grained forest.

Very little has been published on the dynamics of South African forests. At the moment there is therefore no model to predict the grain of a South African forest either for a given environment (e.g. climate and soils) or for forest structure (e.g. whether there is a preponderance of large or small-sized individuals). Midgley *et al.* (1990) indicated that the southern Cape forests [part of White's (1983) Afromontane Forest type] were extremely fine-grained. At the scale of 0.04 ha plots, most species were able to recruit continuously and most canopy species were shade-tolerant. This was interpreted as being due to the unproductive environment (cool climate, poor soils) and conservative disturbance regime (few large gaps) which has favoured shade-tolerant species and restrained both woody and herbaceous shade-intolerant species.

In contrast to the southern Cape forests, our working hypothesis for tropical and subtropical gap-phase forests,

* Division of Forest Science and Technology, Jonkershoek FRC, Private Bag X5011, Stellenbosch 7600.

** Cape Provincial Administration, Umtiza Nature Reserve, P.O. Box 5185, Greenfields 5208—deceased 11 February 1992.

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such as are found at our study site, is that they can be expected to have a greater component of shade-intolerant species, of both herbaceous and woody types. This is due to their situation in a more productive environment (higher temperatures, summer rainfall) which increases the opportunities for regeneration of fast-growing pioneer species. Such forests should therefore be more coarse-grained due to intermittent recruitment of shade-intolerant canopy dominants leading to spatially segregated size classes. Thus an ordination or classification of sample plots using the occurrence of a species in the seedling, sapling or canopy size classes, should reveal spatially distinct groups in a coarse-grained forest. In a fine-grained forest, where species are able to regenerate close to their own adults, data of species occurrence by size class should have little influence on classifications or ordinations.

Our survey was done in a coastal forest of the eastern Cape. According to Acock's (1988) classification these forests appear to fall between the Coastal Tropical Forest Type (Veld Type No. 1) and Valley Bushveld (Veld Type No. 23). White (1983) mapped these forests as the Tongaland-Pondoland Forest type and most recently they have been mapped as Dune Thicket (Lubke, Tinley & Cowling 1988). Information on forest dynamics in the eastern Cape is conspicuous by its absence in the overview of vegetation in the eastern Cape by Lubke, Tinley & Cowling (1988) and in Everard (1987).

Our objectives were to use information from plots to: 1, briefly describe the vegetation; 2, compare ordinations of plots using information on presence/absence of potential canopy species in the seedling, sapling or canopy layers,

to infer grain; and 3, analyse the size-class distributions of the important species to infer their life histories.

STUDY AREA

The study area is situated in the Umtiza Nature Reserve (33°02'S; 27°47'E) which is located on a northeast-facing slope of the Buffalo River Valley, about 10 kilometres from East London. Thicket/forest vegetation covers about 550 ha of the reserve. One of the aims of this reserve is to afford high conservation status to two forest tree species: *Umtiza listeriana* Sim, belonging to a monotypic genus of the Fabaceae, and *Buxus macowanii* Oliv., the box-wood much exploited in the eastern Cape in the past.

Maximum altitude in the reserve is 180 m and many streams dissect the area giving it a variety of aspects. The geology of the area has been mapped as Beaufort Group (Rust 1988) and the soils are mapped as weakly developed soils on rock with black to brown clays and clay loams (Hartmann 1988).

At East London, annual precipitation is 919.2 mm which falls mainly in summer. Mean maximum and minimum temperatures are 22.7°C and 14.0°C respectively. East London is extremely windy (mean wind speed of 4.7 ms⁻¹) as opposed to Cape Town (4.0 ms⁻¹) and George (2.5 ms⁻¹). (Climate information from Weather Bureau, Pretoria.)

METHODS

Sampling

The broad vegetation communities of the Umtiza Nature Reserve were mapped from aerial photographs and essen-

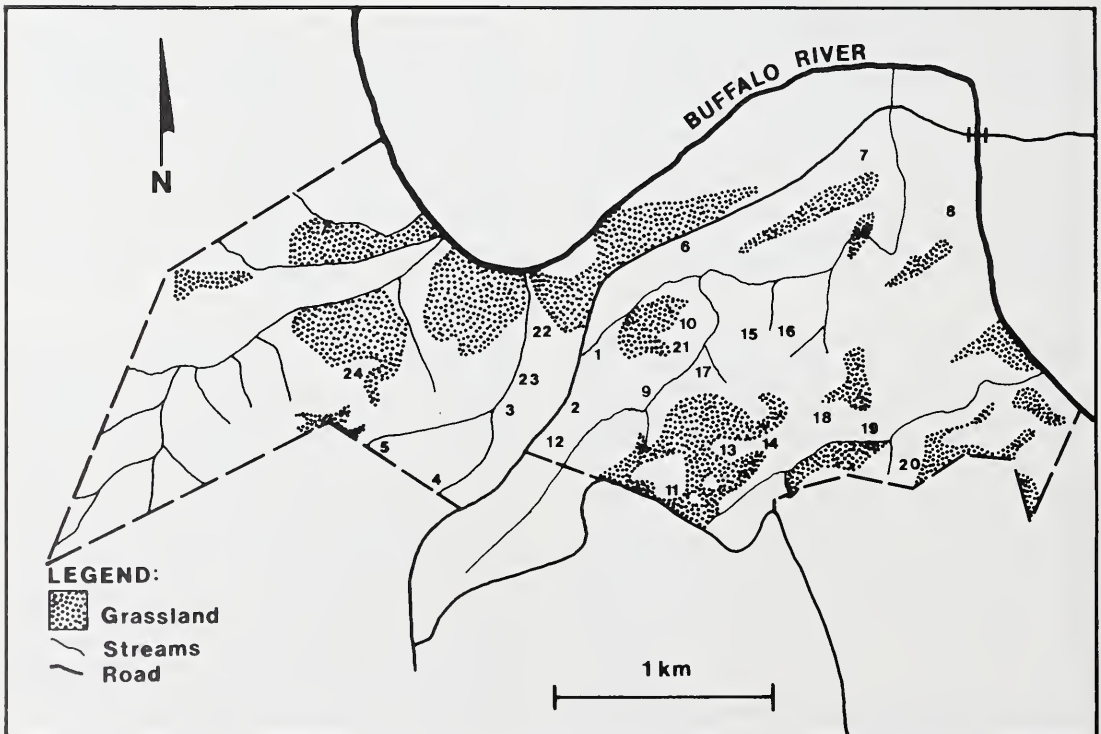


FIGURE 1.—The location of the 24 sample plots at the Umtiza Nature Reserve in the eastern Cape. The shaded-in areas represent *Acacia karroo* grassland and the clear areas forest.

TABLE 1.—A species list, based on 24 sample plots, of the forest vegetation of the Umtiza Nature Reserve

	Numbers of plots		
	Seedlings	Saplings	Canopy individuals
	(0.5–1 m)	(1–5 m)	(> 5 m)
<i>Acacia karroo</i>	—	—	1
<i>Acalypha glabrata</i>	—	—	1
<i>Acokanthera oppositifolia</i>	1	2	1
<i>Allophylus decipiens</i>	11	6	7
<i>Apodytes dimidiata</i>	—	—	2
<i>Brachylaena discolor</i>	7	2	2
<i>B. elliptica</i>	8	5	4
<i>Buxus macowanii</i>	13	12	16
<i>Calodendrum capense</i>	—	—	1
<i>Canthium inerme</i>	4	5	—
<i>Carissa bispinosa</i>	6	8	1
<i>Cassine aethiopica</i>	2	1	2
<i>C. crocea</i>	—	1	5
<i>C. tetragona</i>	2	2	5
<i>Celtis africana</i>	1	1	1
<i>Chaetacme aristata</i>	7	6	12
<i>Clausena anisata</i>	1	1	—
<i>Coddia rudis</i>	2	7	2
<i>Commiphora harveyi</i>	—	1	—
<i>Croton gratissimus</i>	1	1	—
<i>Cussonia spicata</i>	8	12	9
<i>Dalbergia obovata</i>	1	—	4
<i>Diospyros simii</i>	1	1	—
<i>D. dichrophylla</i>	3	2	2
<i>D. whyteana</i>	5	4	4
<i>Dovyalis caffra</i>	2	1	—
<i>D. rhamnoides</i>	—	1	—
<i>D. zeyheri</i>	1	1	—
<i>Ehretia rigida</i>	—	1	—
<i>Ekebergia capensis</i>	1	—	—
<i>Erythrina caffra</i>	1	2	1
<i>Encephalartos altensteinii</i>	—	1	—
<i>Euclea natalensis</i>	10	6	9
<i>E. schimperi</i>	1	1	2
<i>Eugenia capensis</i>	2	2	3
<i>Euphorbia triangularis</i>	1	2	1
<i>Grewia occidentalis</i>	3	2	1
<i>Halleria lucida</i>	—	1	—
<i>Harpephyllum caffrum</i>	4	1	16
<i>Hippobromus pauciflorus</i>	5	2	1
<i>Hyperacanthus amoenus</i>	8	3	3
<i>Ilex mitis</i>	4	3	—
<i>Kiggelaria africana</i>	—	—	1
<i>Maerua racemulosa</i>	12	9	1
<i>Maytenus heterophylla</i>	6	5	7
<i>M. peduncularis</i>	2	2	4
<i>Mimusops obovata</i>	1	1	3
<i>Monanthotaxis caffra</i>	2	3	1
<i>Nuxia congesta</i>	2	—	1
<i>Olea capensis</i>	9	7	5
<i>O. europaea subsp. africana</i>	—	1	1
<i>O. woodiana</i>	10	5	18
<i>Olinia ventosa</i>	1	—	—
<i>Pavetta lucida</i>	—	1	—
<i>Pittosporum viridiflorum</i>	1	1	1
<i>Pleurostyliya capensis</i>	8	2	4
<i>Podocarpus falcatus</i>	—	—	1
<i>Psychotria capensis</i>	—	1	—
<i>Ptaeroxylon obliquum</i>	11	2	17
<i>Rhus chirindensis</i>	2	2	6
<i>R. natalensis</i>	1	1	—
<i>R. undulata</i>	1	—	—

<i>Schotia latifolia</i>	3	—	6
<i>Scolopia mundii</i>	4	3	1
<i>S. zeyheri</i>	6	7	8
<i>Scutia myrtina</i>	4	1	9
<i>Sideroxylon inerme</i>	—	—	1
<i>Strychnos henningsii</i>	—	1	3
<i>Suregada africana</i>	2	3	7
<i>Trichocladus ellipticus</i>	1	1	2
<i>Trimeria grandiflora</i>	—	1	1
<i>Triumfetta pilosa</i> var. <i>effusa</i>	1	—	—
<i>Umtiza listeriana</i>	6	4	11
<i>Vepris undulata</i>	13	3	8
<i>Zanthoxylum capense</i>	11	4	3
<i>Z. davyi</i>	5	3	1

tially two types were found to occur; an *Acacia karroo*/grassland and a thicket/forest type. A grid was placed over a 1:10 000 map of the reserve and 24 sites were selected at random in the forest communities (Figure 1). At each site a square plot of 20 × 20 m was laid out and all woody plants >0.5 m tall were enumerated. These plots were demarcated permanently for further studies on disturbance, mortality and growth. At each sample plot each stem was allocated to one of three size classes: seedlings (0.5–1.0 m in height), saplings (<5 m in height) and canopy (>5 m). Stem diameter at breast height (dbh) was measured for stems >5 m. Identifications were made in the Albany Herbarium, Grahamstown. Nomenclature follows Gibbs Russell *et al.* (1987). The forest canopy ranged from 5–8 m in height with an occasional emergent up to 15 m. At each plot, slope and aspect were noted and two soil samples were taken for standard chemical analyses by the Agricultural Research Institute at Dohne.

Analysis

Initially we classified the forest vegetation using the multivariate package TWINSpan (Hill 1979a), with numbers of stems as the importance values and the default settings of the package. In total about 60 species occurred in the canopy (>5 m in height; Table 1) in our 24 plots. By using species occurrence in seedling, sapling or canopy levels as separate species, we could increase the apparent number of 'species' to about 150 and the apparent number of 'plots' to 72.

In the second part of this study we used multivariate techniques to represent grain or succession in space. Multivariate techniques have long been used for discerning successional trends, e.g. Fox (1990) used community trajectories in multivariate space to study mammal succession over time. We made comparisons between classifications and ordinations of plots but using the two data sets (i.e. 60 spp. versus 150 'spp.' and 24 versus 72 'plots'). The eigenvalues produced by an ordination/classification give an indication of the variance explained by an axis [low eigenvalue (<0.5) = poor separation of samples]. The breadth of an ordination axis gives an indication of the homogeneity amongst samples, with a value of 400 (4 s.d.) indicating that species occurring at one end of an axis are almost completely absent at the other end (Hill 1979b). At this stage there are no rigorous tests for comparing ordinations, although some progress has been made (Grossman, Nickerson & Freeman 1991). We merely visually inspected the package outputs for

differences in eigenvalues and breadth of axes, for the various classifications/ordinations we performed.

We also calculated the position of centroids for ordinations of plots using presence/absence of canopy species in seedlings, saplings and canopy size classes separately. A meaningful successional trajectory would be indicated by significant directional trend in ordination space as defined by information from each size class.

Our expectations were that in a coarse-grained forest, significantly different eigenvalues or breadth of axes would result when data from each size class were used separately, rather than when information about the canopy layer only, was used. We expected centroids to be widely separated in ordination space when species by size-class information was incorporated.

For the second part of the study, the DECORANA (DCA-option)/TWINSPAN packages (Hill 1979a, b) were again used. Presence/absence (due to the great discrepancies in numbers of stems amongst size classes) was used as the importance value, and again we used the default settings of the package.

RESULTS

Environmental data

Soil colours recorded included very dark brown, dark red-brown, dark brown and brown-black, and soil texture was sandy clay loam. The soils also had a relatively high pH and calcium content (Table 2). Slopes were mostly gentle and aspect was predominantly between 90° and 270°.

Vegetation description

Very little phytosociological data have been published on the eastern Cape forests and thickets. Furthermore, vegetation patterns are complex (see Acocks 1988). For this reason we have appended an annotated species list (Table 1). The maximum number of stems observed per 0.04 ha sample for the canopy size class was 74, for seedlings it was 454 and for saplings 25. The maximum number of seedlings per sample plot was high for the following species: *Praeroxylon obliquum* (421), *Buxus macowanii* (189) and *Ilex mitis* (256). Species richness per 0.04 ha of woody plants ranged from 13–36.

The separation of the forest into types, based on abundance of canopy individuals, was weak (eigenvalue =

TABLE 3.—Sample plots belonging to first two groups, and associated eigenvalues, produced by TWINSPAN using presence/absence data for canopy species (60 spp.) and canopy species in three size classes separately (about 150 spp.)

Only canopy species	Canopy species per size class
(eigenvalue = 0.26)	(eigenvalues = 0.29)
group 1 (sample plots) 17, 9, 21, 19, 24, 11, 18, 22, 23, 14, 20, 13, 15, 16	group 1 (sample plots) 13, 15, 16, 17, 14, 22, 18, 24, 11, 20, 23, 19, 9, 21
group 2 (sample plots) 3, 2, 4, 6, 12, 1, 5, 10, 7, 8	group 2 (sample plots) 3, 7, 8, 4, 6, 12, 1, 2, 5, 10

0.376). Furthermore, axis 1 was only a maximum of 2.5 s.d. units broad and axis 2 only 2.3 s.d. units. This probably reflects the overlapping distribution of the common species and many rare species (Table 1). Down-weighting for rare species made a negligible difference in eigenvalues. We have taken this weak separation of types and small spread in ordination space of the forest to indicate that only one vegetation community was present. Most of the canopy species are well represented in the seedling and sapling (Table 1) size classes. Essentially the forest is dominated by *Praeroxylon obliquum*, *Harpephyllum caffrum*, *Olea woodiana*, *Chaetacme aristata*, *Umiza listeriana* and *Buxus macowanii* (see Table 1).

Vegetation dynamics

The groupings of samples produced at the first division using 60 species (i.e. only canopy species) versus 150 species (i.e. canopy species per size class separately), whilst having different orderings, were identical (Table 3) and both had similar and small eigenvalues (0.26 compared to 0.29). This indicates that species by size-class data do not produce a different classification or a different separation of samples.

The ordination using 72 'plots' and the 60 canopy species shows considerable overlap of the three size-class groups (Figure 2A, B, C). This is clearly depicted by the similarity of position of each centroid and their relatively close proximity to the origin. There is no suggestion of orderly directional trend of movement of centroids. This could indicate that there is no consistent difference in successional status amongst plots. The spread along the first ordination axis is narrow (about 3 s.d.) and the eigenvector was also small (0.279).

Size-class distribution

Most of the common canopy species have typical inverse J-shaped size-class distributions (Table 4). To this group could be added many of the less common species we encountered but which had similar size-class distributions. This includes species such as *Maytenus heterophylla*, *M. peduncularis*, *Cussonia spicata*, *Euclea natalensis*, *Brachylaena elliptica* and *Olea capensis* subsp. *capensis*.

DISCUSSION

We interpret the multivariate analysis to indicate that this subtropical forest is fine-grained. This forest is there-

TABLE 2.—Environmental information pertaining to the study area. For slope and aspect classes, numbers represent numbers of plots. Values in brackets indicate the variance

Slope classes			
0–10°	10–20°	20–30°	
13	7	4	
Aspect classes			
0–90°	91–180°	181–270°	271–360°
2	8	8	6
Soil chemistry (means)			
pH	%C	Na (ppm)	Ca (ppm)
5.5 (0.3)	195 (0.3)	0.9 (0.2)	14.2 (46.7)

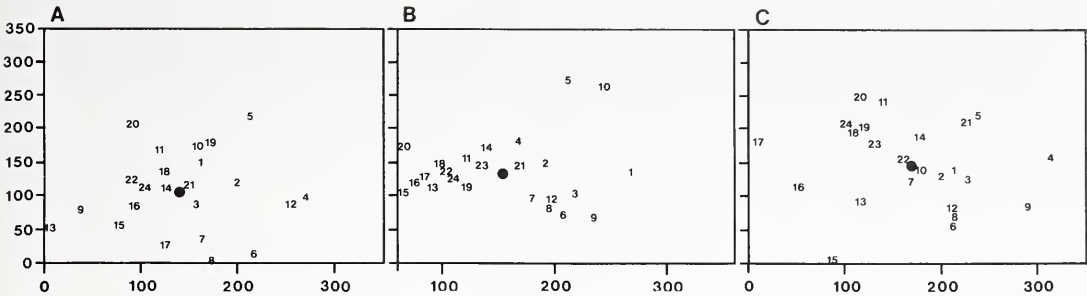


FIGURE 2.—Ordination diagrams using woody species in size classes: A, canopy; B, seedling; C, sapling. All 72 plots were ordinated together but represented separately for clarity. The dots indicate the centroids. In A, samples 22 and 23 are superimposed.

TABLE 4.—Numbers of individuals per size class of the most common canopy species encountered in the Umtiza Nature Reserve

Species	Height (m)		dbh (cm)						
	0.6–0.99	1–5	<10	<15	<20	<25	<30	<35	>35
<i>Buxus macowanii</i>	1 045	279	305	63	13	2	—	—	—
<i>Olea woodiana</i>	123	29	44	26	16	14	12	10	8
<i>Ptaeroxylon obliquum</i>	947	4	16	16	16	11	3	—	2
<i>Umtiza listeriana</i>	46	25	32	15	9	7	1	4	2
<i>Vépris undulata</i>	221	58	8	3	4	—	—	2	2
<i>Scolopia zeyheri</i>	38	18	11	3	2	—	1	—	—
<i>Harpephyllum caffrum</i>	18	2	9	4	3	4	2	4	9
All stems	3 867	1 229	679	206	100	66	36	27	42

fore fairly similar to the more temperate southern Cape forests (Midgley *et al.* 1990). Both have an abundance of species with inverse J-shaped size-class distributions and co-occurrence of different size classes within a species. These results indicate that large-scale disturbances are not important in determining community composition of both these forest types.

From a conservation perspective, because the shifting mosaic of structural phases (*sensu* Whitmore 1989) is fine-grained (or stationary) at Umtiza, relatively small patches of forest may be viable because most species can regenerate on a small spatial scale. Obviously, other factors need to be taken into account (edge effects, visits by dispersers) to complete the picture. We predict that the disturbance regime at Umtiza will be conservative (preponderance of small gaps) and that advance regeneration will inherit most gaps.

Finally, it is clear from this survey that *Umtiza listeriana* and *Buxus macowanii*, the two species of special conservation importance, are both abundant and apparently regenerating adequately. They appear to be well conserved in the Umtiza Reserve.

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The vegetation of the northeastern Orange Free State, South Africa: physical environment and plant communities of the Ea land type

H.C. ECKHARDT*, N. VAN ROOYEN* and G.J. BREDEKAMP*

Keywords: Braun-Blanquet method, classification, geology, Grassland Biome, land types, soils

ABSTRACT

The research was carried out in the Ea land type of the northeastern Orange Free State, with the objective of reclassifying and refining Acocks's veld types. TWINSpan classification results were further refined by Braun-Blanquet procedures. The 100 relevés distributed over the Ea land type resulted in the recognition of four major vegetation types which may be divided into nine plant communities. The communities were hierarchically classified, described and ecologically interpreted. DECORANA ordination was used to determine vegetation/environmental gradients and relationships.

UITTREKSEL

Navorising is gedoen op die Ea-landtipe in die noordoostelike Oranje-Vrystaat met die doel om Acocks se veldtipes te herklassifiseer en te verfyn. Die resultate van die TWINSpan-klassifikasie is met behulp van Braun-Blanquetprosedures verder verwerk. Die 100 relevés wat oor die hele Ea-landtipe versprei is, het vier hoofplantegroei-tipes opgelewer wat in nege plantgemeenskappe onderverdeel kan word. Die gemeenskappe is hiërargies geklassifiseer, beskryf en ekologies geïnterpreteer. Plantegroei- en omgewingsgradiënte is met behulp van DECORANA-ordening bepaal.

CONTENTS

Introduction	117
Study area	117
Geology	118
Physiography	119
Soils	119
Climate	120
Methods	120
Description of communities	121
1. <i>Artemisia afra</i> – <i>Rhus dentata</i> shrubland of the slopes	121
1.1 <i>Hyperthelia dissoluta</i> – <i>Eragrostis curvula</i> shrubland of steep slopes	121
1.2 <i>Hyparrhenia hirta</i> – <i>Diospyros lycioides</i> shrubland of moderate slopes	121
2. <i>Themeda triandra</i> – <i>Elionurus muticus</i> grassland of relatively dry undulating midslopes/plains	124
2.1 <i>Elionurus muticus</i> – <i>Trachypogon spicatus</i> grassland of relatively dry, rocky, shallow soils ..	124
<i>Vernonia oligocephala</i> – <i>Trachypogon spicatus</i> grassland of relatively dry, rocky, shallow soils	124
<i>Harpochloa falx</i> – <i>Trachypogon spicatus</i> grassland of relatively moist, rocky, shallow soils ..	124
2.2 <i>Microchloa caffra</i> – <i>Elionurus muticus</i> grassland of relatively moist soils	124
<i>Tristachya leucothrix</i> – <i>Elionurus muticus</i> variation	124
<i>Heteropogon contortus</i> – <i>Eragrostis plana</i> variation	124
3. <i>Themeda triandra</i> – <i>Eragrostis plana</i> transitional dry/wet grassland	124
4. <i>Eragrostis plana</i> – <i>Eragrostis curvula</i> wet/moist grassland	124

4.1 <i>Eragrostis curvula</i> – <i>Setaria sphacelata</i> moist grassland	125
4.2 <i>Eragrostis plana</i> – <i>Paspalum distichum</i> wet grassland	125
Ordination	125
Conclusion	125
Acknowledgements	127
References	127

INTRODUCTION

The Grassland Biome of South Africa covers approximately 27% of the country. As a result of intensive agricultural practices and urbanization, together with industrialization, the deterioration of the grassland led to concern amongst decision-makers, resulting in the launch of the Grassland Biome Project (Mentis & Huntley 1982). This project aims at developing a better knowledge and understanding of the grasslands of South Africa to permit efficient land-use planning, utilization, conservation and management. To reach these goals, it is necessary to reclassify Acocks's (1988) Veld Types. This reclassification means a more detailed identification, description and mapping of the present grassland types (Scheepers 1986). The northeastern Orange Free State was identified as an area for which little or no phytosociological data exist. This study will also contribute to the syntaxonomic synthesis presently being undertaken by the Botany Department of the University of Pretoria (Bredenkamp *et al.* 1989; Kooij 1990; Fuls *et al.* 1992a, b; Bezuidenhout 1988).

STUDY AREA

The total study area is situated in the northeastern corner of the Orange Free State, i.e. between 29° 00' and 29° 47' E longitude and 27° 00' and 28° 00' S latitude, bordering Transvaal and Natal (Figure 1). It covers approximately 5 600 km² and comprises five land types, namely land types A, B, C, E and F (Land Type Survey Staff 1984), which can be further subdivided (Figure 2).

* Department of Botany, University of Pretoria, Pretoria 0002.
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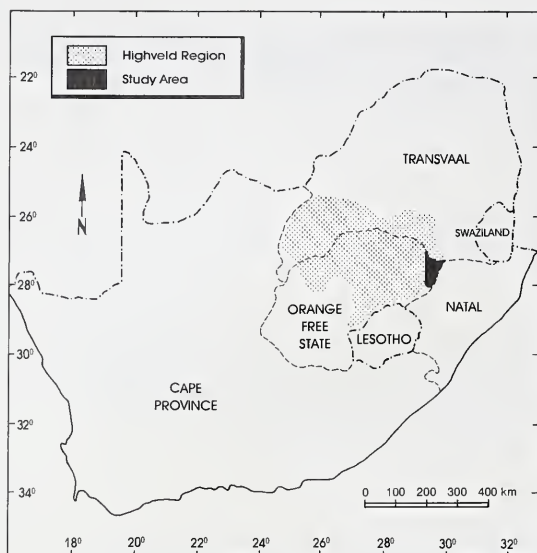


FIGURE 1.—Map of South Africa indicating the total study area situated in the Highveld Region.

One third of the area (184 000 ha) is covered by the Ea land type which is dealt with in this report. The other land types are to be discussed in detail in later papers. A land type is an area which is uniform with respect to terrain form, soil pattern and climate. Towns situated in the area are Vrede and Memel (Land Type Survey Staff 1984). According to Acocks (1988), the study area represents six veld types: Patchy Highveld to *Cymbopogon-Themeda*

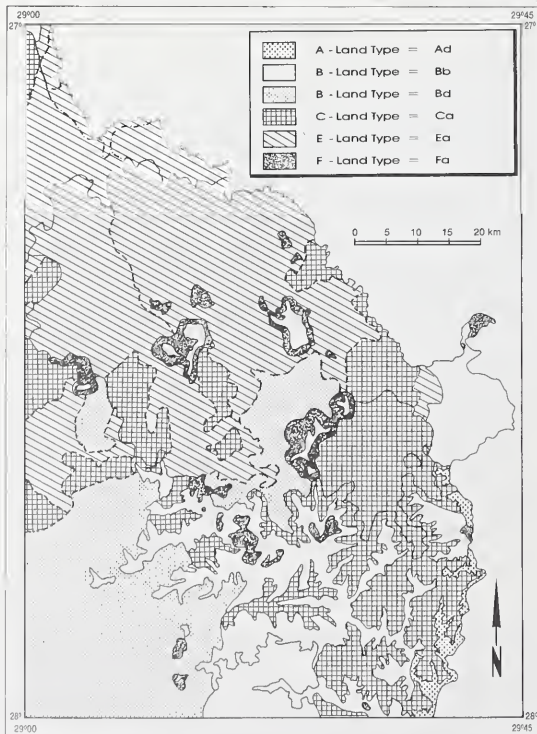


FIGURE 2.—Map indicating the distribution of the different land types (Land Type Survey Staff 1984).

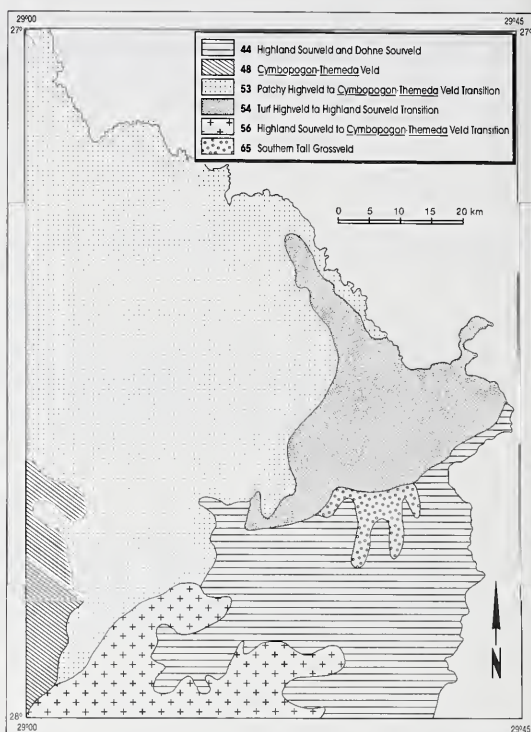


FIGURE 3.—The distribution of the different veld types within the total study area according to Acocks (1988).

Veld Transition (No. 53), covering approximately 50% of the total study area, is restricted to the northern and central parts. The Highland Sourveld (No. 44) stretches along the Natal border in the east. Smaller patches of *Cymbopogon-Themeda* Veld (No. 48) and Highland Sourveld to *Cymbopogon-Themeda* Veld Transition (No. 56) occur in the southwestern and southern parts. The Turf Highveld to Highland Sourveld Transition (No. 54) stretches over the central eastern part, while one isolated patch of Southern Tall Grassveld (No. 65) occurs to the south of Memel (Figure 3).

GEOLOGY

KAROO SEQUENCE

The Karoo Sequence occupies the total study area (Figure 4). Two important groups which can be distinguished here, are the Ecça and Beaufort Groups. The Clarens, Elliot and Molteno Formations are also part of this sequence, but they are limited in extent.

Ecça Group

This group is restricted to the north and northeastern parts of the study area, bordering Transvaal (Figure 4). The Ecça Group can be subdivided into a Lower Ecça sandstone and shale, a Middle Ecça shale, and an Upper Ecça sandstone and shale [South African Committee for Stratigraphy (SACS) 1980]. Ecça shales are in general dark grey and carbonaceous. Ecça sandstone was deposited in an aquatic environment.

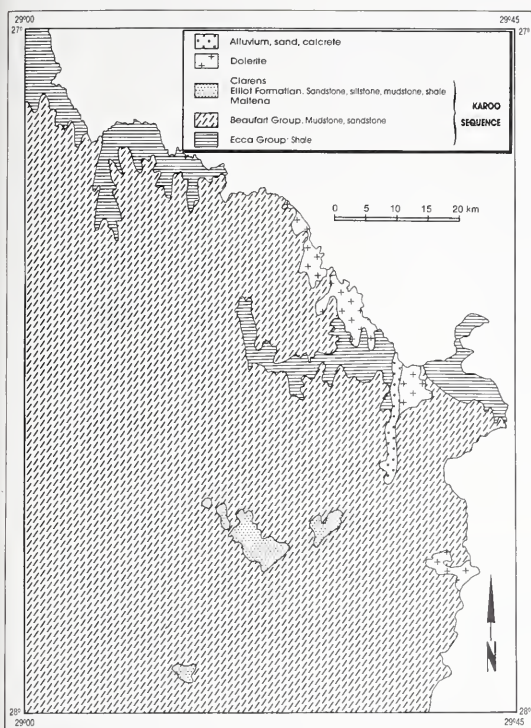


FIGURE 4.—The geology of the total study area (adapted from Dept. of Mineral and Energy Affairs 1984).

Beaufort Group

The Beaufort Group covers more than 80% of the study area. It can be subdivided into three subdivisions, namely the Lower, Middle, and Upper Beaufort Beds. The argillaceous rocks are massive or blocky weathered. The mudstones are greenish grey, blue-grey or red. Cross-bedded sandstones are common.

Clarens Formation

The Clarens Formation, previously known as Cave Sandstone, is a massive, fine-grained rock type, which reaches a thickness of up to hundreds of metres. Under weathering conditions, this formation features fantastic shapes in the form of pillars and caves. Exposed surfaces are white or cream-coloured, whereas its base is pink or deep red. A few isolated hills in the central and southern part of the study area have the characteristic shapes of this formation as described above. The main components are subangular to rounded grains of quartz and subordinate feldspar. The accumulation of sandstone is probably of aeolian origin, being re-arranged later by flowing water (Du Toit 1954).

Elliot Formation

Purple and red mudstones and shales, together with red sandstones and thick beds of yellow and white feldspathic sandstones are characteristic of this formation (Du Toit 1954). It is well distinguished by its prevailing colouration as can be seen on the slopes of the few koppies in the study area.

Molteno Formation

This formation is distinguished by the typical grey and blue colouration of the shales, and the coarse grain and 'sparkling' appearance of the dominating sandstones. Between Harrismith and Memel the Molteno Formation occurs only as a single thin grit, covered by the Elliot Formation and underlain by the Beaufort Group (Du Toit 1954).

Alluvium, sand, calcrete

Alluvium and sand are more recent by-products of erosion, most probably originating from the Beaufort Group (pers. obs.). A narrow strip of these deposits, together with calcrete, occurs in the Seekoeivlei area, which is drained by the Klip River (Department of Mineral and Energy Affairs 1984).

Dolerite

The dolerites intruded the sediments of the Karoo Sequence during the last stages of the Drakensberg volcanicity. These intrusions are either horizontal, evenly inclined or undulating sheets (SACS 1980). The dolerite dykes are restricted to the eastern part of the study area.

PHYSIOGRAPHY

The study area is part of the inland plateau region or highveld (Figure 1) and consists of plains with moderate relief to closed hills and mountains with moderate and high relief (Kruger 1983; Mentis & Huntley 1982). The altitude is between 1 500 and 2 000 m with some peaks reaching heights of up to 2 200 m. There is a clear gradient in the physiography of the area from south to north. Three broad divisions can be distinguished.

The southern and eastern parts are characterized by isolated hills and mountains with moderate and high relief. The middle part is depicted by lowlands, hills and mountains with a moderate to high relief. This part can further be described as strongly undulating irregular land, gradually changing over into plains with moderate relief. These plains are slightly irregular, undulating, with occasional hills scattered over the area. This region is most suitable for cultivation purposes, whereas the rest of the area is more suited to cattle farming.

The Drakensberg forms a clear watershed, separating the tributaries of the Vaal River, west of the escarpment, from the tributaries of the Tugela River, east of the escarpment. The study area is situated in the catchment area of the Vaal River. The Klip River is the main drainage line into which several smaller rivers and spruits flow (Figure 5). The northern part of the study area is mainly drained by the Spruitsonderdrift and Kommandospruit, which are both perennial streams. There is a gradual flattening towards the north, resulting in less deeply incised low to moderate undulating plains in the north. These are in strong contrast to the deeply incised mountainous southern part.

SOILS

According to Land Type Survey Staff (1984), the soils are undifferentiated and can have one or more of either vertic, melanic and red structured diagnostic horizons. The names and descriptions of the different soil forms are

TABLE 1.—The mean monthly temperatures and extreme temperatures (°C) for two weather stations closest to the study area

	Frankfort						Standerton					
	1985–1990						1985–1990					
	Max.	Min.	Max.	Date	Min.	Date	Max.	Min.	Max.	Date	Min.	Date
Jan.	28.3	14.8	36.4	18-01-73	4.0	30-01-61	27.3	14.4	37.2	05-01-29	2.5	05-01-60
Feb.	27.0	13.9	36.1	27-02-83	4.4	28-02-65	26.5	14.0	35.0	15-02-84	3.3	20-02-24
Mar.	26.5	11.3	35.0	03-03-84	0.6	10-03-74	26.0	12.4	34.0	03-03-84	0.6	15-03-30
Apr.	23.5	7.5	31.5	05-04-83	-4.0	27-04-55	24.2	8.8	31.7	01-04-33	-5.3	30-04-17
May	21.6	1.0	29.0	02-05-79	-7.5	19-05-84	21.3	2.7	30.0	03-05-33	-10.6	31-05-18
Jun.	18.1	-2.9	24.6	09-06-83	-11.0	20-06-57	17.6	-1.1	25.0	01-06-32	-12.8	11-06-07
Jul.	18.6	-3.7	23.8	29-07-60	-12.0	23-07-54	18.5	-2.1	26.1	31-07-40	-12.8	18-07-13
Aug.	21.8	0.4	27.9	19-08-77	-10.0	14-08-55	21.7	1.7	29.9	30-08-22	-11.7	16-08-13
Sep.	23.3	5.2	33.7	29-09-83	-8.3	09-09-74	23.6	5.9	34.4	30-09-23	-7.8	16-09-30
Oct.	24.8	9.3	34.2	30-10-65	-1.9	21-10-65	24.6	9.5	35.2	21-10-61	-3.8	01-10-13
Nov.	26.1	12.1	35.6	07-11-68	1.4	15-11-76	25.6	11.5	34.4	06-11-68	-1.1	25-11-12
Dec.	27.3	13.5	36.0	31-12-84	1.1	06-12-84	26.5	13.5	37.4	31-12-82	2.2	08-12-70
Av.	23.9	6.9					23.6	7.6				

used according to the Soil Classification Working Group (1991). The Glenrosa and Mispah Forms are restricted to terrain units 1 and 2 and very often occur together to form a complex. These soils are shallow (< 200 mm) and have a low clay content (15–20%) and are mostly not arable. Terrain units 3 and 4 are characterized predominantly by pedocutanic, lithocutanic and yellow-brown apedal B horizons. Soils are relatively deep (> 350 mm) and have a higher clay content (> 35%). Although the Ea land type is generally more suitable for crop production than the rest of the study area, large areas are non-arable because of the high clay content of the soils. Terrain unit 5 is characterized by either rock and alluvium or the vertic Rensburg and Arcadia soil forms. The last two forms have a high clay content (> 55%) and are deep (> 500 mm).

CLIMATE

Rainfall

The study area is situated in the summer rainfall zone with an average annual rainfall of 750 mm. Precipitation takes place mostly in the form of thunderstorms, between November and March. Midsummer droughts occur towards the end of December until middle of January (Department of Agriculture and Water Supply 1986). Rainfall data for weather stations at Frankfort and Standerton are given in Figure 6 (Weather Bureau 1986).

Temperature

Mean annual maximum and minimum temperatures for the period 1985–1990 and extreme temperatures recorded at Frankfort and Standerton are given in Table 1. The frost period extends from April to October, which means a frost-free period of approximately 150 days a year (Weather Bureau 1986).

METHODS

Relevés were compiled in 100 stratified random sample plots. Stratification was based on terrain units (De Beer

1988; Land Type Survey Staff 1984). Sampling of the different terrain units was done on a subjective basis. Five different topographical positions were distinguished, namely 1 = crests, 2 = scarps, 3 = midslopes, 4 = foot-slopes and 5 = valley bottoms, floodplains or drainage lines (Land Type Survey Staff 1984). Minimum plot sizes of 16 m² are considered to be adequate for grassland surveys (Scheepers 1975). Nevertheless, it was decided to fix the plots at 100 m² because of the large scale on which this survey was conducted, and to ensure that scarce, possible diagnostic species were included. This

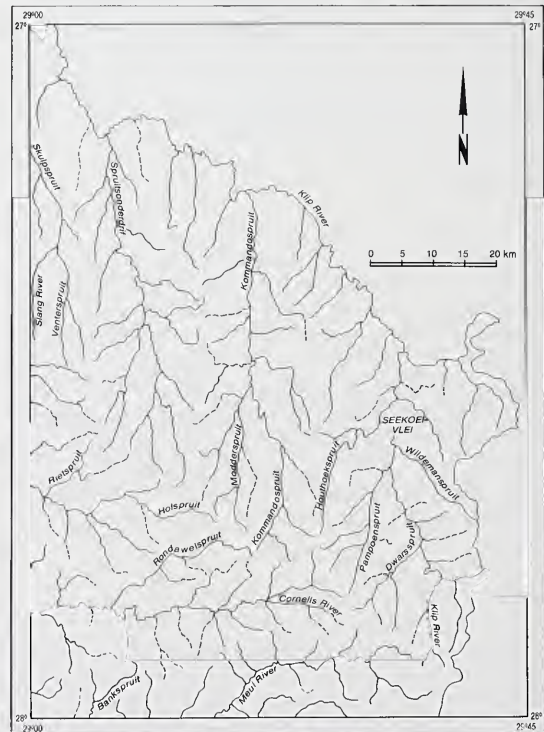


FIGURE 5.—The drainage of the total study area with the Klip River as main drainage line.

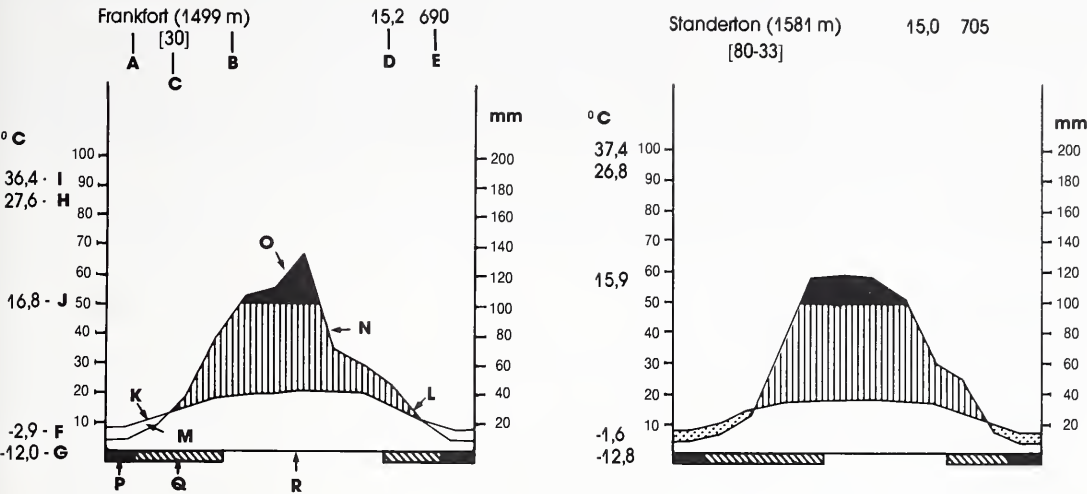


FIGURE 6.—Climatic diagrams for two weather stations. A, station; B, height above sea level; C, duration of observations in years (indicates temperature and precipitation respectively); D, mean annual temperature in °C; E, mean annual precipitation in mm; F, mean daily minimum temperature (coldest month); G, lowest temperature recorded; H, mean daily maximum temperature (hottest month); I, highest temperature recorded; J, mean daily temperature fluctuation; K, mean monthly temperature; L, mean monthly precipitation; M, dry season; N, wet season; O, very wet season (mean monthly precipitation >100 mm); P, cold season (mean daily minimum below 0°C); Q, month with absolute minimum below 0°C; R, frost-free period (Weather Bureau 1986).

is essential for efficient Braun-Blanquet type data processing and also in accordance with the aim of identifying areas for possible conservation. The floristic composition in each sample was determined by using the Braun-Blanquet cover-abundance scale (Mueller-Dombois & Ellenberg 1974). In accordance with Werger (1973), scale-unit 2 was divided as follows: A, covering 5–12% of the sample plot area and; B, covering 13–25% of the sample area. Taxon names conform to those of Gibbs Russell *et al.* (1985 & 1987). Structural classification was according to Edwards (1983). The following habitat data were recorded in each sample plot: geology, topography, terrain unit, slope and aspect, rockiness, soil types and erosion.

To derive a first approximation of the vegetation types, two-way indicator species analysis (TWINSPAN) (Hill 1979a) was applied. This was further refined by Braun-Blanquet procedures (Behr & Bredenkamp 1988; Bredenkamp *et al.* 1989). The results obtained are presented in a phytosociological table (Table 2). Detrended correspondence analysis (DECORANA) (Hill 1979b) was applied to the floristic data set to determine vegetation gradients and illustrate vegetation/environmental relationships.

DESCRIPTION OF COMMUNITIES

The Ea land type is characterized mainly by the constant presence, mostly with high cover-abundance values of *Themeda triandra*, and *Eragrostis curvula* and *E. plana* (species group L, Table 2). The number of species recorded in the relevés varies between 15 and 25, with an average of 19 species.

1. *Artemisia afra*–*Rhus dentata* shrubveld

This shrubveld is situated on moderate to steep scarps (30°–90°) (terrain unit 2) facing rivers and streams

(Figure 7). Shallow, rocky soils of the Glenrosa and Mispah Forms are typical of this terrain type (Figure 8). The average rock size is more than 500 mm in diameter, covering more than 20% of the surface. Clear signs of erosion can be observed, which are ascribed mainly to the steepness of the slopes. The utilization of the vegetation by dassies (*Procavia capensis* Pallas 1766) is apparent in some areas.

The vegetation is characterized by species group C (Table 2) and the diagnostic species include the shrubs *Artemisia afra*, *Rhus dentata* and *Diospyros austro-africana*. *Bidens pilosa* and *Hibiscus trionum* are weeds and are often associated with disturbed areas. Dominant woody species are the diagnostic shrub species. Conspicuous and dominant grasses include *Themeda triandra*, *Eragrostis curvula* and *E. plana* of species group L, and *Aristida congesta* and *A. junciformis* of species group I (Table 2). The herbaceous layer of terrain unit 2 is more conspicuous and better developed than those of other terrain units.

1.1 *Hyperthelia dissoluta*–*Eragrostis curvula* shrubveld

This shrubveld is situated on steeper (40°–90°) slopes and displays patches of bare soil with a relatively high degree of erosion (Figures 7 & 8). Diagnostic species include the dominant grass species *Hyperthelia dissoluta*, the forbs *Clutia natalensis*, *Garuleum woodii*, *Sutera polelensis*, the xerophytic fern *Pellaea calomelanos* and the grass *Melica racemosa* (species group A, Table 2). *Themeda triandra*, *Eragrostis curvula* and *E. plana* are among the most constantly present companion grass species occurring in this community. An average of 15 species was recorded per sample plot.

1.2 *Hyarrhenia hirta*–*Diospyros lycioides* shrubveld

This shrubveld is characterized by species group B (Table 2) and can be further distinguished from the

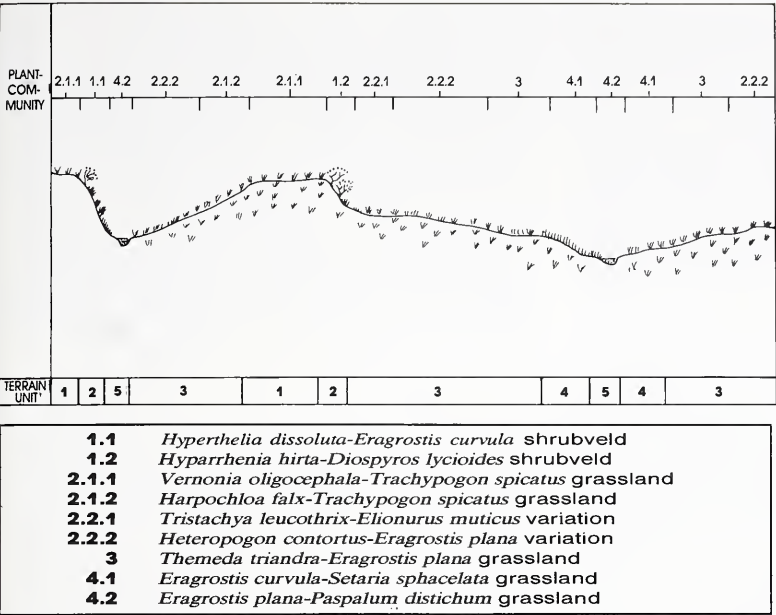


FIGURE 7.—A schematic representation of the terrain units with the associated plant communities identified in the Ea land type.

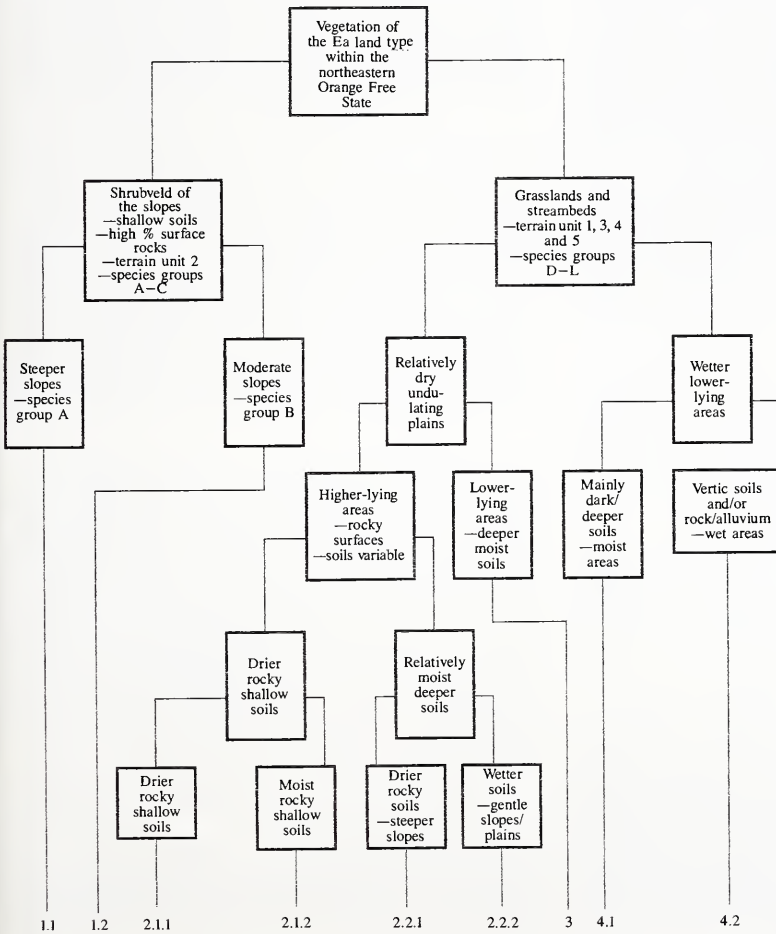


FIGURE 8.—Hierarchical diagram to indicate the prominent habitat characteristics which are associated with the respective plant communities.

Hyperthelia dissoluta–*Eragrostis curvula* shrubveld by the presence of conspicuous and constantly present grass species of species group I (Table 2). Diagnostic species include the tall and dominant grass species *Hyparrhenia hirta*, the shrubs *Diospyros lcyoides*, *Grewia occidentalis* and *Heteromorpha trifoliata* and the weedy *Zinnia peruviana* and *Monsonia angustifolia* (species group B, Table 2). A further characteristic of this community is the presence of seral and pioneer species listed in species group I, for example the grasses *Aristida junciformis*, *A. congesta* and *A. bipartita*. An average of 23 species was recorded per sample plot.

2. *Themeda triandra*–*Elionurus muticus* grassland

This plant community is to a great extent similar to grasslands described by Bezuidenhout (1988) and Kooij (1990), except for the prominence of *Eragrostis plana* and other species typical of the moister eastern grasslands of the Orange Free State. This community compares well to the *Elionurus muticus*–*Themeda triandra* alliance described by Fuls *et al.* (1992a). This grassland type covers more than 60% of the Ea land type enclosed by the study area. A great diversity of soil forms occur, including Mispah, Glenrosa, Mayo, Inhoek, Westleigh, Swartland, Clovelly, Oakleaf, Glencoe, Bonheim and Arcadia. Soil depth varies from 100 to more than 700 mm. Deeper soils (> 500 mm) display higher clay contents (35–55%). Most of these soils have been ploughed, and cultivated lands replace this grassland community to a great extent (Figure 7).

This grassland is characterized by species group G (Table 2) and the diagnostic grass species are the prominent and conspicuously present *Elionurus muticus*, *Heteropogon contortus*, *Eragrostis capensis*, *E. racemosa*, *Brachiaria serrata*, *Helictotrichon turgidulum*, *Aristida diffusa* and *Trichoneura grandilumis*. Diagnostic forbs are *Crabbea acaulis* and *Berkheya onopordifolia* (Table 2). Other prominent species are *Themeda triandra*, *Eragrostis plana* and *E. curvula*, while the asteraceous forbs *Helichrysum rugulosum* and *Berkheya pinnatifida* are conspicuously present.

2.1 *Elionurus muticus*–*Trachypogon spicatus* grassland

This grassland is situated on terrain unit 1 and the higher-lying parts of terrain unit 3, with low to moderate slopes (2°–30°) (Figure 7). Soils are shallow (< 300 mm) (Figure 7) and have a relatively low clay content.

Species group D (Table 2) characterizes this grassland and includes the diagnostic co-dominant grass species *Trachypogon spicatus*, as well as the forbs *Acalypha punctata*, *Striga bilabiata* and *Polygala hottentotta* (Table 2). Prominent species include *Elionurus muticus*, *Themeda triandra*, and *Eragrostis curvula*.

Two variations can be distinguished, namely the *Vernonia oligocephala*–*Trachypogon spicatus* variation and the *Harporchloa falx*–*Trachypogon spicatus* variation. These two variations are distinguished by the presence of species groups E and F respectively (Table 2). No clear differences in the habitat can be found to explain the occurrences of the two variations, but soil moisture regime seems to be decisive in the delimitation of the two variations.

2.2 *Microchloa caffra*–*Elionurus muticus* grassland

This grassland covers the largest part of the Ea land type within the study area with respect to the other plant communities. It occurs on a wide range of soil types, for example vertic Arcadia to orthic Glenrosa Forms. This grassland occurs on crests, slopes and plains (Figure 7). The terrain as a whole is gently undulating with slopes of 0°–8°. Overgrazing, especially by sheep, often results in patches of bare soil, which are prominent in this grassland. The reason for patch-overgrazing is the disproportionate utilization of the veld, resulting in patches being over-utilized (Fuls 1992). These patches are gradually retrograding until bare patches of soil develop.

This grassland is the typical form of the *Themeda triandra*–*Elionurus muticus* grassland and is characterized by the presence of species group G and the absence of species group D (Table 2). Dominant grass species include *Elionurus muticus*, *Heteropogon contortus*, *Eragrostis curvula*, *Themeda triandra* and *Eragrostis plana*. The forb *Helichrysum rugulosum* is constantly present but less conspicuous. An average of 20 species was recorded per sample plot. Two variations can be distinguished, the *Tristachya leucothrix*–*Elionurus muticus* and *Heteropogon contortus*–*Eragrostis plana* variations. The former is characterized by the presence of species group F, and is further distinguished from the other variation by a higher percentage surface rock and lower soil moisture regime (Figure 8). The *Heteropogon contortus*–*Eragrostis plana* variation is clearly distinguished by higher cover-abundance values for *Eragrostis curvula* and *E. plana* (Table 2), indicating a higher soil moisture content with respect to the former variation.

3. *Themeda triandra*–*Eragrostis plana* dry/wet grassland

This grassland represents a transitional zone between relatively dry and wet grasslands, separating the relatively drier communities on the higher-lying terrain units from the relatively moister communities on the lower-lying terrain units (Figure 7). The soils are deep (> 500 mm) and moist (Figure 8). Overgrazing in this grassland can be observed to a lesser extent in the form of bare soil patches, but rather as dense patches of *Eragrostis plana*, invading the disturbed areas.

The transitional grassland is differentiated by the presence of species groups H and I, and the absence of species group G (Table 2). No diagnostic species could be identified for this grassland. The dominant species include *Eragrostis plana*, *Themeda triandra*, *Eragrostis curvula* and *Aristida bipartita*. The herbaceous layer is not well developed and open and includes species such as the forbs *Helichrysum rugulosum* and *Berkheya pinnatifida*, indicating a degree of degradation. An average of 15 species per sample plot was recorded, indicating a decrease in species diversity with an increase in soil moisture.

4. *Eragrostis plana*–*Eragrostis curvula* wet grassland

This grassland represents the vegetation falling within moist to wet areas, including footslopes and drainage lines (Figure 7). The areas adjacent to drainage lines, display gentle slopes (0°–5°) and subsequently show few signs

of erosion. Rivers and streams in contrast, often used by cattle and sheep as drinking places, frequently show serious signs of erosion. Seasonal and perennial water pans occur widely scattered over the area, often attracting a variety of birds. These pans are also accessible to cattle and sheep. Since most of the rivers and streams flow throughout the year, they may be used by stock at any time.

This grassland is characterized by species group J (Table 2), and the diagnostic grass species are *Paspalum dilatatum*, *Cynodon dactylon*, *Eragrostis micrantha*, and the forbs *Conyza sumatrensis*, *Pseudognaphalium oligandrum*, *Helichrysum dregeanum* and *Cephalaria scabiosa* (Table 2). Two communities can be distinguished.

4.1 *Eragrostis curvula*–*Setaria sphacelata* moist grassland

This grassland represents the vegetation found in moist areas adjacent to drainage lines, and is transitional to grassland (Figure 7). This is indicated by the presence of species groups H and I, which are differential species for this community. Soils are deep (> 500 mm) and without any surface rocks. These areas are not suitable for cultivation due to the high clay content (> 55%) of the soils. Cover-abundance values for the diagnostic and dominant species are relatively high, indicating a dense vegetation cover.

Conspicuous and constant species are the grasses *Eragrostis curvula*, *Aristida bipartita*, *Setaria sphacelata*, *Themeda triandra* and *Eragrostis plana*, as well as the forbs *Berkheya pinnatifida* and *Hermannia depressa* (Table 2). An average of 17 species was recorded per sample plot.

4.2 *Eragrostis plana*–*Paspalum distichum* wet grassland

This grassland represents the vegetation found along rivers, streams and pans (Figure 7). Riverbeds and streambeds are degraded to a large extent, often displaying bare rock surfaces and alluvium (Figure 8). Soils found here are of the Rensburg Form, being deeper than 500 mm. Few widely spaced pans do occur in the area; they are restricted to depressions. Trampling effects by cattle and sheep are noticeable especially on the margins of these pans, where the animals normally drink. The vegetation in these marginal zones is clearly disturbed.

A decrease in species diversity can be observed, if the species-richness of this community is compared with that of other vegetation types. This grassland is characterized by species group K (Table 2), and the diagnostic species include the grasses *Paspalum distichum*, *Cymbopogon excavatus* and *Diplachne fusca*, the herbs *Cyperus longus*, *Mariscus congestus*, *Bidens bipinnata*, *Chenopodium ambrosioides*, *Argyrolobium pauciflorum*, *Juncus exsertus*, *Sium repandum*, *Deverra burchellii*, *Gerbera ambigua*, *Cyperus marginatus* and *Schoenoplectus decipiens* (Table 2). Other conspicuous species are the grasses *Eragrostis plana*, *Cynodon dactylon*, *Paspalum dilatatum* and *Eragrostis micrantha*, and the herbs *Pseudognaphalium oligandrum* and *Conyza sumatrensis*.

The herbaceous layer is prominent, but not dominant to the grass layer. The presence of species group K and the simultaneous absence of species groups H and I distinguishes this community from the *Eragrostis curvula*–

Setaria sphacelata grassland. An average of only 13 species was recorded per sample plot.

ORDINATION

Figure 9 represents the distribution of all 100 relevés along the first and second axes of a DECORANA ordination. No discontinuities are observed and by inspection it is clear that the vegetation communities are distributed along a moisture/trophic gradient. This gradient is extracted by the first axis of the DCA ordination. McDonald (1987) found in his study on the vegetation of the Swartboschkloof that soil moisture played a secondary role next to the major role being played by soil geology. In his study on the vegetation of the mire Northern Kisselbergmosen, SE Norway, Okland (1990) found that depth to the water table had a major influence on the distribution pattern of the vegetation. The communities found under extreme conditions, namely the dryland and wetland communities, occur on the periphery of the diagram. The dryland community is represented by the *Artemisia afra*–*Rhus dentata* shrubveld, occurring on dry, sandy, dystrophic soils to the top left of the diagram.

The wetland community, *Eragrostis plana*–*Eragrostis curvula* grassland, occurs on wet, clayey, eutrophic soils to the right of the diagram. The *Themeda triandra*–*Elionurus muticus* and *Themeda triandra*–*Eragrostis plana* grasslands are situated in an intermediate position. No separation occurs in Figure 9, concerning the last two grassland types. A gradient along the second axis can also be observed. Communities at the top of the axis occur on scarps and slopes, whereas the bottom part represent communities occurring on undulating terrain.

Figure 10 represents an ordination of only the *Themeda triandra*–*Elionurus muticus* grassland. The relevés of variations 2.2.1 and 2.2.2 are more or less situated to the right of the relevés of community 2.1. The fact that no clear discontinuity can be observed emphasizes the indistinct, gradual change from dryland to wetland communities associated with the gradually undulating terrain. Relevés to the right of the diagram are situated on wetter lower-lying bottomland areas with deep, clayey vertic soils. The left part of the diagram represents drier higher-lying areas with shallow, sandy orthic soils. No gradient can be observed along the second axis.

CONCLUSION

The application of Braun-Blanquet procedures to refine the results of the TWINSPLAN classification was successful. Four major vegetation types were identified, which are further subdivided into nine plant communities. These units do exist in practice and can be incorporated in veld management programmes.

It is of the utmost importance that the farmer considers each unit on its own and that management programmes take into account the characteristics of each unit (see Eckhardt *et al.* submitted). Communities, which are considered as having conservation value, are those occurring on steep slopes (40°–90°) adjoining wet grassland communities. The *Hyperthelia dissoluta*–*Eragrostis curvula* shrubveld and *Eragrostis plana*–*Paspalum*

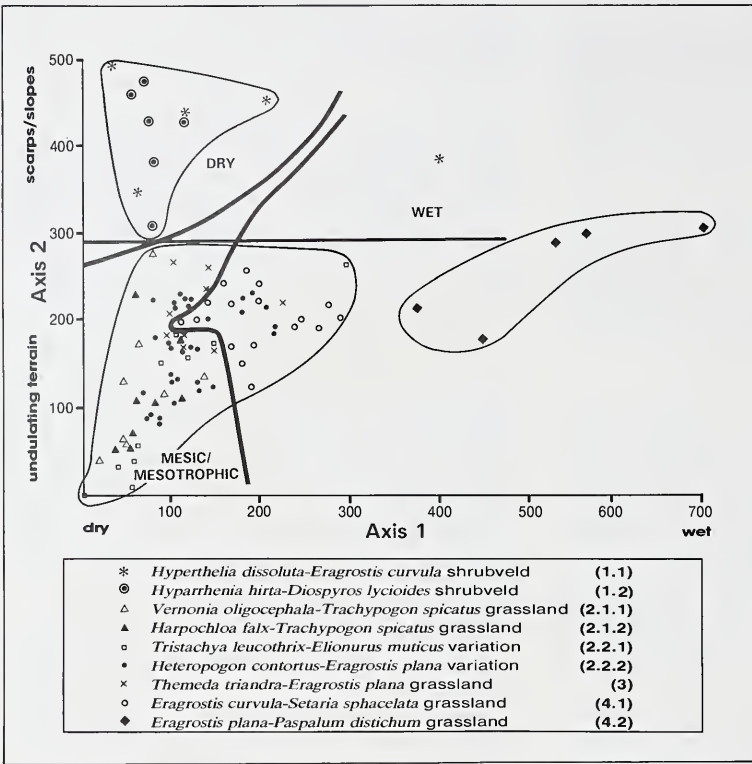


FIGURE 9. — A scatter diagram of the ordination of the vegetation on the Ea land type.

distichum grassland together form a complex in some areas, which is worthwhile conserving. Some of these areas are partly or totally inaccessible to cattle and sheep and therefore still remain in a relatively undisturbed state.

The results obtained by ordination (DECORANA) indicate the response of vegetation types to different

environmental conditions. Moisture and trophic regimes have a strong influence on the distribution of vegetation types. A correlation between these two habitat factors and the vegetation can be observed. The application of the Braun-Blanquet method for the B, C and F land types should result in the identification of many more vegetation units, since these land types appear to be heterogeneous with respect to their topography.

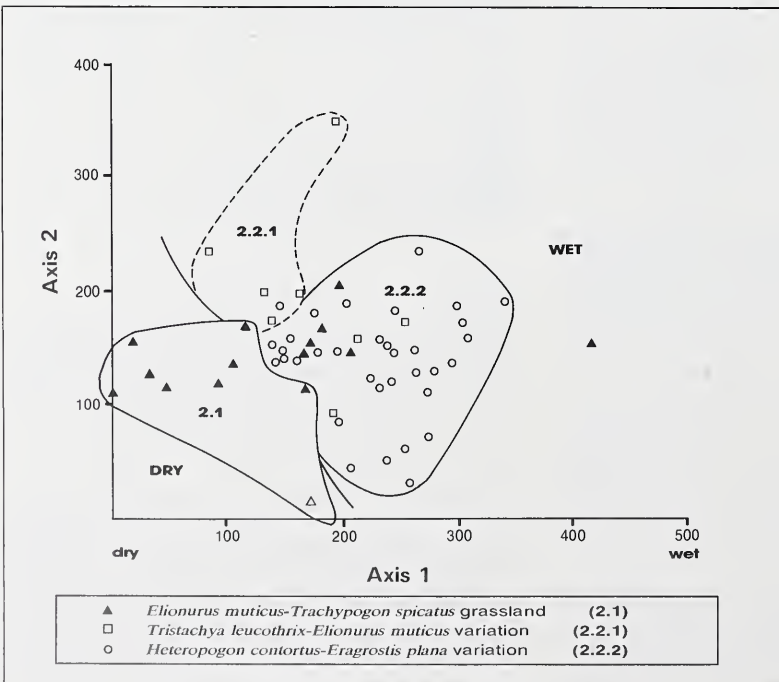


FIGURE 10. — A scatter diagram of the ordination of plant community 2.

If farmers are to benefit practically from the results obtained in this study, it is advisable to bring to their attention the diagram presented in Figure 8. This diagram serves as an important key for the delimitation of vegetation types and habitat units, which are to be managed in accordance with the characteristics of each.

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The vegetation of the southern Langeberg, Cape Province. 1. The plant communities of the Boosmansbos Wilderness Area

D. J. MCDONALD*

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ABSTRACT

An analysis of the fynbos shrublands and forests of the Boosmansbos Wilderness Area, southern Langeberg, Cape Province, South Africa, is presented. Data were collected at 119 sites in mature fynbos vegetation (>10 years old) and at five sites in patches of Afromontane Forest. Emphasis was placed on the fynbos shrublands and sample sites were subjectively located along a transect from south to north across the Langeberg range in the study area. This south to north orientation follows a complex gradient of changes in aspect, slope, geology, soil form and climate. Data were initially analysed using TWINSpan and the resulting classification refined using Braun-Blanquet procedures. One forest subassociation and 12 fynbos communities were identified and described. A proposed hierarchical classification of the fynbos communities is presented.

UITTREKSEL

'n Analise van die fynbos en woude van die Boosmansbos Wildernisgebied, suidelike Langeberge, Kaapprovinsie, Suid-Afrika, word aangebied. Data is van 119 monsterpersele in volwasse fynbosplantegroei (> 10 jaar oud) en vyf monsterpersele in Afro-montane woude versamel. Klem is op die fynbosstruikveld gelê en monsterpersele is subjektief langs 'n transek van suid na noord oor die Langeberge in die studiegebied uitgelê. Die suid tot noord oriëntasie volg 'n komplekse gradiënt van veranderings in aspek, helling, geologie, grondform en klimaat. Data is aanvanklik d.m.v. TWINSpan ontleed en die resultaat met behulp van Braun-Blanquet-prosedures verfyn. Een woudsubassiasie en 12 fynbosgemeenskappe is geïdentifiseer en beskryf. 'n Hiërgariese klassifikasie van die fynbosgemeenskappe word voorgestel.

CONTENTS

Introduction	129
Study area	130
Location	130
Physiography	130
Geology	131
Soils	131
Climate	132
Methods	133
Vegetation	133
Afromontane Forest	137
Fynbos	137
1. <i>Erica hispidula</i> Shrublands	139
1.1 <i>Erica hispidula</i> – <i>Spatalla mubicola</i> Shrublands (A)	139
1.2 <i>Erica hispidula</i> – <i>Restio inconspicuus</i> Shrublands	139
1.2.1 <i>Restio inconspicuus</i> – <i>Anthochortus crinalis</i> Shrublands (B)	140
1.2.2 <i>Restio inconspicuus</i> – <i>Protea grandiceps</i> Shrublands (C)	141
1.2.3 <i>Restio inconspicuus</i> – <i>Protea aurea</i> subsp. <i>aurea</i> Shrublands (D)	141
1.2.4 <i>Restio inconspicuus</i> – <i>Hypodiscus aristatus</i> Shrublands (I)	142
1.2.4.1 <i>Hypodiscus aristatus</i> – <i>Leucadendron eucalyptifolium</i> Shrublands (E)	142
1.2.4.2 <i>Hypodiscus aristatus</i> – <i>Berzelia intermedia</i> Shrublands	144
1.2.4.2.1 <i>Berzelia intermedia</i> – <i>Erica melanthera</i> Shrublands (F)	144

1.2.4.2.2 <i>Berzelia intermedia</i> – <i>Erica blenna</i> var. <i>blenna</i> Shrublands (G)	144
1.2.4.3 <i>Hypodiscus aristatus</i> – <i>Erica versicolor</i> Shrublands (H)	145
2. <i>Cannomois parviflora</i> Shrublands	146
2.1 <i>Cannomois parviflora</i> – <i>Leucadendron eucalyptifolium</i> Shrublands	146
2.1.1 <i>Leucadendron eucalyptifolium</i> – <i>Protea lorifolia</i> Shrublands (J)	146
2.1.2 <i>Leucadendron eucalyptifolium</i> – <i>Siaberoha cernua</i> Shrublands (K)	147
2.2. <i>Cannomois parviflora</i> – <i>Passerina obtusifolia</i> Shrublands	148
2.2.1 <i>Passerina obtusifolia</i> – <i>Leucospermum calligerum</i> Shrublands (L)	148
2.2.2 <i>Cannomois parviflora</i> – <i>Passerina obtusifolia</i> Shrublands 'Typicum' (M)	149
Discussion and conclusions	149
Acknowledgements	150
References	150

INTRODUCTION

The position of the Langeberg on the west-east axis of the Cape Fold Belt places it between the mountains of the southwestern Cape and those of the southern Cape (Figure 1). It therefore forms an important highland phytogeographical link between the montane floras of these respective regions.

The southern Langeberg is defined as the Langeberg Range between Kogmanskloof and the Gouritz River. The description and classification of the plant communities of the Boosmansbos Wilderness Area presented in this paper form part of a broad-scale phytosociological study of the southern Langeberg.

* National Botanical Institute, P.O. Box 471, Stellenbosch 7599.
Present address: Conservation Biology Unit, NBI Kirstenbosch, Private Bag X7, Claremont 7735.
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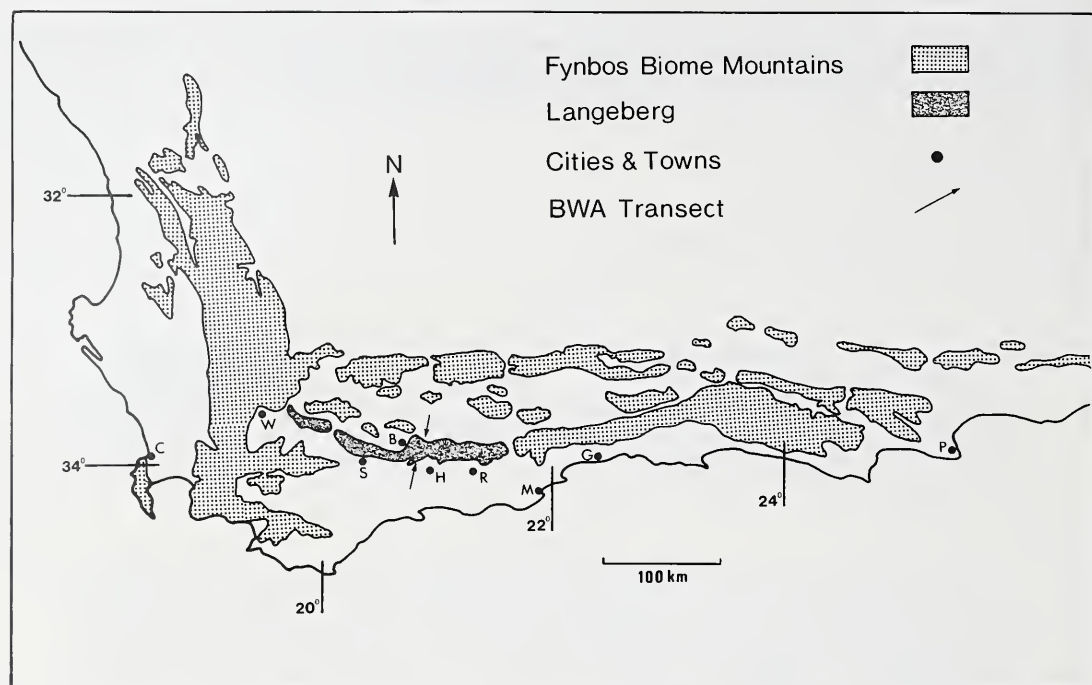


FIGURE 1.—Map of the mountains of the Fynbos Biome showing the position of the Langeberg and the location of the Boosmansbos Wilderness Area (BWA): B, Barrydale; C, Cape Town; G, George; H, Heidelberg; M, Mossel Bay; P, Port Elizabeth; R, Riversdale; S, Swellendam and W, Worcester.

Separate papers cover the description and classification of the vegetation of two other similar transects at Swellendam and Bergfontein (near the Gouritz River) (McDonald 1993a & b).

STUDY AREA

Location

The Boosmansbos Wilderness Area (BWA) near Heidelberg, Cape Province, is more or less centrally situated in the southern Langeberg and extends across its widest part (13 km). The area forms part of the Grootvadersbosch State Forest and was proclaimed a wilderness area in 1978. The mountain catchments are managed for conservation, limited-access recreational hiking and production of potable water. The Duivenhoks River has its origins in these catchments.

The BWA is approximately 14 200 ha in extent. It is bounded on the south side by agricultural land, on the north side by a private nature reserve and on the west and east sides by privately owned mountain land.

An access road, the Barend Koen Road, traverses the area from the lower south slopes, adjoining the farm Goedehoop, to Helderfontein at 1 150 m. The road is used for management and forms part of the hiking trail network in the area. During this study the road and paths gave ready access to the area for sampling purposes.

The transect was arbitrarily delimited through the centre of the BWA, straddling the Barend Koen Road on the south slopes and the path to Witbooisrivier on the north slopes. It does not follow a straight line over the mountain range

but was positioned to cover as much topographical variation and plant community variation as possible. The transect area was approximately 3 000 ha.

Physiography

The southern plateau-like footslopes of the Langeberg in the BWA are deeply incised by the Duivenhoks River. At higher elevations, fault valleys such as Vaalrivierkloof, Bobbejaankloof, Platbosrivierkloof and Saagkuilkloof, which feed the Duivenhoks River, are encountered. Saagkuilkloof and Platbosrivierkloof fall within the delimited transect and have north- and south-facing slopes. North of Platbosrivierkloof is Repeater Kop, a high west-east ridge lying approximately between Vaalrivierkloof and Helderfontein. Behind (north of) Repeater Kop is the Helderfontein Valley and north of that a high ridge runs westwards from Grootberg. The Moeras River and Helderfontein Stream start at the watershed behind Repeater Kop. Moeras River drains northwestwards towards Barrydale. Grootberg is the highest peak (1 627 m) in BWA and directly below it is the deep Boosmansbos Valley. The stream from Helderfontein runs through this valley, through a gorge below Noukrans Peak (1 443 m) and Horingberg (1 487 m) to join the Duivenhoks River outside the wilderness area.

North of Grootberg is a series of sandstone ridges with interspersed shallow valleys. There is one main, relatively broad valley with a shallow gradient eastwards towards Brandrivier. North of the valley is Deception Ridge, so named because of its deceptive height. The north slopes of Deception Ridge are steep and rocky, giving way lower down to mesa-like plateaus of gravels and sandstone conglomerate (see below).

Geology

The Langeberg is one of the west-east trending mountain ranges with northward-verging folds, in the eastern zone of the Cape Fold Belt. It consists mainly of sediments of the Table Mountain Group (Cape Supergroup) and in part, of pre-Cape Malmesbury Group sediments. The range was formed during the Cape orogeny when the rocks of the Cape Supergroup were folded in a single phase, multiple event orogeny of Permian to Late Triassic age (De Villiers 1944; Hålbich *et al.* 1983). The core of folding in the Langeberg is at Tradouw Pass where the massive folding has resulted in what Le Roux (1974) describes as the Langeberg megastructure.

A transect over the Langeberg at any given locality has its own peculiar local geology owing to folding, faulting and consequent positioning of strata and fault valleys. Only one detailed geological study of a section of the Langeberg exists (Le Roux 1974, 1983). Fortuitously this coincides in part with the area proclaimed as BWA and with the vegetation sampling transect chosen for this study.

Five formations of the Table Mountain Group are found in the study area. The Peninsula Formation sandstone makes up the southern slopes from about 400–1 600 m a.s.l. At 1 150 m the Cedarberg Formation is represented by a relatively thin band of shale in the vicinity of Helderfontein. It is deeply incised and eroded at the headwaters of the Moeras and Duivenhoks Rivers.

North of the Cedarberg Formation are the sandstone sediments of the Nardouw Subgroup comprising the Goudini, Rietvlei and Skurweberg Formations. For the purposes of this study, the Nardouw Subgroup is equated with the Peninsula and Cedarberg formations since the finer distinctions are of secondary importance. Nardouw Subgroup sandstone is also found on the south side of the mountain between Tradouws Pass and Grootvadersbosch Forest Station, Ertjiesvlei and in a narrow band eastwards from below Horingberg to beyond Palmyra (Le Roux 1974, 1983). However, Nardouw sandstones were not encountered on the south side of the range on the vegetation transect as designated in BWA.

Above Witbooisrivier, on the north side of the transect, high terrace gravels are found (Lenz 1957; Le Roux 1974). These gravels are cemented by a siliceous matrix, forming resistant silcrete caps or duricrusts (Schloms *et al.* 1983) and are remnants of the African Erosion Surface (Partridge & Maud 1987).

Gravels of the Enon Formation are found at the southern extremity of the vegetation transect. Le Roux (1974) described the Enon sediments as 'weakly consolidated gravels and mudstones in alternating strata ... composed of vein quartz, quartzite (derived from the Table Mountain Group), greenish sandstones and shales (apparently from the Bokkeveld Group), as well as conglomerates older than the Enon Formation.'

Soils

The soils of BWA agree with the general pattern described by Campbell (1983) for southern Cape coastal mountains and the classification follows the system of the Soil

Classification Working Group (SCWG 1991). The soil forms encountered, their positions in the landscape and their relationship to the geological formations are outlined below.

Oakleaf Form

Soils of this form have an orthic A-horizon over a diagnostic neocutanic B-horizon. The detailed definition of a 'neocutanic' horizon is given by SCWG (1991); briefly it is a horizon derived from recent sediments and other unconsolidated materials. It shows little colour differentiation and weak structural development.

At low altitude (350 m), at the southern extremity of the BWA vegetation transect, Oakleaf Form soils are encountered. These soils result from the weathering of Enon Formation sediments (see above). At one site (Relevé 59) on the Cedarberg Formation shale at Helderfontein, the soil was identified as Oakleaf Form. This soil has formed by weathering of shale in a moist situation as opposed to the formation of a Clovelly Form soil (described below) under slightly drier conditions.

Cartref and Houwhoek Forms

Cartref and Houwhoek Form soils are found from low (425 m) to high (1 600 m) elevations on south-facing slopes, mainly on parent rock of the Peninsula Formation. The form encountered at any position in the landscape is dependent on the land facet (convexity or concavity), its steepness and consequent drainage. The Houwhoek Form soils display weak ferrihumic character in the B-horizon and are very close to the more common Cartref Form soils with lithocutanic B-horizons, showing no podzolization.

Champagne Form

Champagne Form soils are found at sites where drainage is impeded and where deep accumulation of organic matter has occurred. This soil form is typically found at 'seeps' where Restionaceae form dense, matted peat-like deposits. On some of the high peaks (e.g. Grootberg, 1 627 m) and ridges (Repeater Kop, 1 506 m) Champagne Form soils are found on south aspects, on steep slopes. The slopes have a mean gradient of 30° and organic material has accumulated to an average depth of 700 mm. Podzolization may occur in the parent rock beneath, but this would presumably have little influence on the vegetation which is rooted in the humus.

Mispah Form

At sites where bedrock is close to the surface and where soil development is poor (due to a combination of excessive drainage, high insolation, low organic matter accumulation), Mispah Form soils with shallow orthic A-horizons over hardrock are found. This form is found on the high-altitude north-facing slopes of Repeater Kop ridge, Grootberg and on the terraced gravel-conglomerates above Witbooisrivier.

Glenrosa Form

Soils of the Glenrosa Form are also found on the north aspect of the ridges and peaks of BWA but on the middle

to lower slopes. Here the form is diagnosed by presence of Orthic A and Lithocutanic B-horizons. This form typically occurs on the well-drained terraced ridges of the Nardouw Subgroup strata north of Grootberg.

Clovelly Form

Clovelly Form soils are found at three different localities in BWA. These soils with a Yellow-Brown Apedal B diagnostic horizon below an Orthic A-horizon have mainly but not exclusively resulted from accumulation of transported material. The exception is on the Cedarberg Formation shaleband near Helderfontein where the *in situ* shale, with its fine-grained matrix has weathered to Clovelly Form soils.

The south-facing slope of the ridge west of Grootberg is a debris slope of Nardouw Subgroup sandstone. These slopes which lie above the contact with the Cedarberg Formation and which are moderately well-drained, exhibit Clovelly Form soils (Relevé 64).

In the eastward-trending intermontane valley north of Grootberg, deposits of material eroded from Nardouw Subgroup sandstones have given rise to well-developed Clovelly Form soils. These soils are well drained and in one pit examined (Relevé 130) pieces of reworked ferricrete were found at 700 mm depth. On Deception Ridge (north-most ridge on the transect), the south-facing terraced slopes have a mixture of Clovelly and Glenrosa Forms depending on the presence or absence of apedal and lithocutanic B-horizons respectively.

Climate

Local climate of the Boosmansbos Wilderness Area is poorly documented. A rainfall recording station is situated at Grootvadersbosch Forest Station (Strawberry Hill), however, this inadequately reflects rainfall as it occurs and changes in the montane environment along the BWA transect. The limited data available at best reflect low-altitude conditions on the south slopes. Fuggle (1981) warns of the dangers of interpolation between climatic stations. However, since no climate measurements were made during this study, limited available data from Weather Bureau records (Strawberry Hill 025/599) and Fuggle (1981) are used to obtain at least seasonal trends in climate. Mean annual precipitation estimates were obtained from isohyet maps prepared by Dent *et al.* (1987).

Wind

In summer the prevailing winds from the southeast and southwest influence the Boosmansbos Wilderness Area the most. The onshore, moisture-laden southeast winds are trapped by the Langeberg and orographic rain occurs. During the winter the winds blow primarily from the northwest and southwest also bringing rain following cold fronts. Berg winds occur in winter heralding the approach of cold fronts (Fuggle & Ashton 1979; Fuggle 1981; Heydorn & Tinley 1980; Tyson 1964, 1969).

Temperature

Temperature data for the study area are non-existent. This situation is commonly found since few weather stations are situated in the Cape mountains (Bond 1981; Fuggle & Ashton 1979; Fuggle 1981). Temperatures in

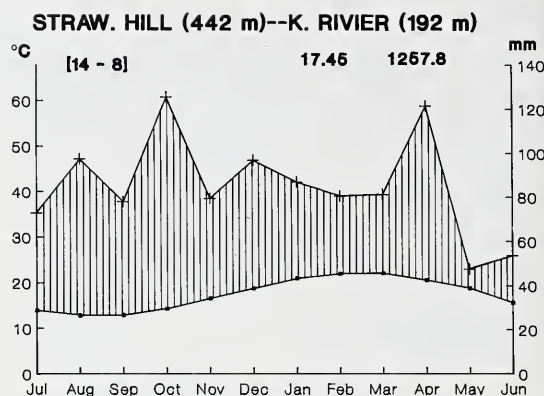


FIGURE 2.— Walter-Lieth climate diagram representing the climate on the southern slopes of the Boosmansbos Wilderness Area. Rainfall data from Strawberry Hill (Grootvadersbosch Forest Station) and temperature data from the nearest station at Karringmelksrivier, near Heidelberg.

mountain areas vary considerably from place to place; therefore it is only possible to make generalized statements about the effect of latitude and altitude on temperature (Fuggle 1981.)

The nearest reliable temperature data are from Karringmelksrivier (192 m a.s.l.) near Heidelberg, well away from the BWA. However, these data are used to give general trends in seasonal temperature variation. In Figure 2 they are combined with rainfall data from Strawberry Hill to give an approximation of the climate of the southern slopes of the BWA.

Precipitation

Precipitation in the BWA occurs mostly as rain. However, fog or mist from low stratus cloud plays a considerable, but unmeasured, role in contributing to total precipitation. Snowfalls occur in September, October and occasionally November.

As for other climatic parameters, rainfall is not measured on a regular basis in the study area. It is clear from observation that topography and aspect significantly affect rainfall distribution. Interpolated data from Dent *et al.* (1987) show that the lower south slopes of the study area receive approximately 600 mm mean annual precipitation. With an increase in altitude this value increases to almost 1 300 mm on the high peaks. The largest part of the study area receives 1 000 mm precipitation on average each year. With a decrease in altitude on the north slopes, bordering the Little Karoo, a steep gradient exists, with the lower slopes receiving less than 300 mm mean annual precipitation (nearby Barrydale receives 276 mm p.a.; Fuggle 1981).

The seasonal distribution of rainfall on the south aspects of the study area are reflected in the data from Strawberry Hill weather station, and on the lower north slopes by data from Klein Doornrivier, Figure 3. No month is without rain but most rain falls in spring and autumn. Rainfall results from post-frontal anticyclonic (onshore) air movement over the subcontinent from August to November. In the autumn months of March, April and May rainfall results from the progression of cold fronts along the

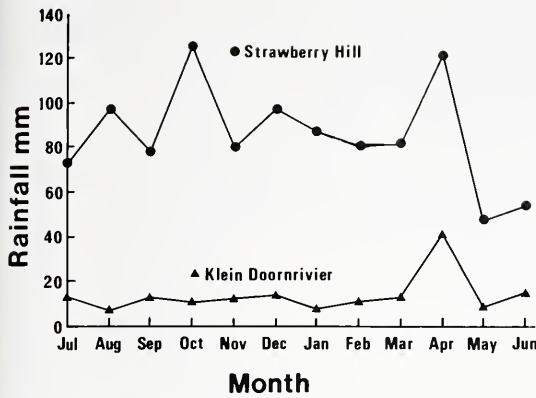


FIGURE 3.—Mean monthly rainfall at Strawberry Hill (1978–1990) and Klein Doornrivier (1982–1990) located at the lower south and north extremes of the Boosmansbos sample transect respectively. Rainfall peaks occur in spring (October) and autumn (April) at Strawberry Hill and in autumn at Klein Doornrivier.

southern coast. Occasional cut-off lows occur which may result in extensive rains (Van Heerden & Hurry 1987), affecting rainfall over the Langeberg as well.

Solar radiation

No measured data are available for incoming solar radiation on the slopes of the Langeberg. However, estimates of incoming radiation will be obtained from the RADSLOPE model (Schulze & Lambson, unpublished) and presented in a later paper (McDonald, unpublished).

Bond (1981) calculated potential radiation for a range of slopes and aspects for 33° 30' south latitude using Swift's (1976) algorithm. Incoming radiation in summer was shown to be similar on all slopes and aspects, whereas in winter steep north slopes receive the highest and steep south slopes the lowest radiation. This is true for the Langeberg, and since the range lies between 33° 30' and 34° South, Bond's results could safely be extrapolated here. Similar to the Outeniqua Mountains and the Swartberg, the Langeberg is also often capped with cloud, further limiting incoming radiation, particularly on the high-elevation south slopes.

METHODS

Methods employed in sampling the vegetation of Boosmansbos Wilderness Area follow those of McDonald (1983, 1988) where rectangular plots of 5 × 10 (50 m²) were used to sample fynbos shrublands; 5 × 10 m plots are commonly used in surveys of fynbos (e.g. Boucher 1978; Bond 1981; Campbell 1985; Boucher 1987). The long axis of each plot was oriented parallel with the contour, with the plot being subdivided into 10 equal-sized subplots to facilitate data recording.

In Afromontane forests circular plots with a radius of 11.3 m (≈ 400 m²) were used to collect both floristic and structural data (Geldenhuys *et al.* 1988; Knight 1989).

Only permanently recognizable species were recorded. Geophytes such as *Bobartia* spp. were recorded and included in the analyses. In general 'ephemeral' geophytes and annuals encountered were noted but not used in the analyses. The Braun-Blanquet (BB) cover-abundance scale was applied as shown in Tables 1 & 2. The midpoint of

the BB values given as percentage cover is as follows: 5 = 87.5%; 4 = 62.5%; 3 = 37.5%; 2 = 15.0%; 1 = 2.5%; + = 0.1%; R = value ignored (Mueller-Dombois & Ellenberg 1974; Werger 1974). A border zone of 1.5 m from the perimeter of each plot was searched for any species not found in the marked plot. Species occurring outside the plot are represented by 'O' in the phytosociological tables. Structural data were collected where the strata and their respective cover (BB scale) were recorded at each sample site. The structural characters of stems (e.g. woody, herbaceous) and leaves (e.g. simple, cupressoid, sclerophyllous, leptophyllous) were also evaluated using the BB scale.

TWINSPAN (Hill 1979) was used for initial analysis of the floristic data. The classification was then refined further by sorting the phytosociological tables with the aid of PCTables (Boucher unpublished).

Boosmansbos Wilderness Area is the only area of the Langeberg for which 1:20 000 colour aerial photography is available (Job 824). It was therefore possible to stratify the study area, identify major land type/vegetation units and predetermine general location of plot positions in these units prior to fieldwork. Precise positions of sample plots were subjectively determined with plots placed in stands of mature fynbos (>10 years old).

Floristic composition of communities was compared using diagnostic or character species of each community as the main criteria. Those communities that were not immediately obviously equivalent were subjectively judged on the basis of character species, taxonomic relatedness or morphological similarity e.g. *Berzelia lanuginosa* found in the southwestern Cape versus *B. intermedia* found on the Langeberg, in similar habitats. These relationships do not reflect strict 'synonymy' but serve as a guide for future synthesis of communities found in fynbos vegetation.

VEGETATION

Boosmansbos Wilderness Area is named after the well-preserved Afromontane Forest patch in the deep ravine below Grootberg Peak. There are a number of other smaller patches of forest below Repeater Kop as well. These forest patches represent one vegetation type of limited extent in the study area. Shrubby fynbos covers the greater proportion of BWA and is described in greater detail.

Muir (1929) recognised three major categories of fynbos in the Langeberg: 1, The Succession of Bare Rock Surfaces and Cliffs; 2, The Sclerophyllous Vegetation of the Langeberg; and 3, The Langeberg Forest and Mountain Streams. In the present study emphasis is placed on the Sclerophyllous Vegetation which Muir subdivided into (a) Heath, (b) Macchia (c) (Vegetation of ...) Upper Southern Slopes and Summit and (d) (Vegetation of ...) Northern Slopes and Base.

The fynbos communities are described in the order of the proposed classification. Each community is given a species-binomial name which has no syntaxonomic hierarchical rank (McDonald 1988). The communities are placed in context in the Fynbos Biome (see Rutherford & Westfall 1986) by attempting to relate them to communities described by other workers; based on both floristic and structural similarities. The structural formation of each

Table 1. A phytosociological table of the *Erica hispidula* Shrubland Communities south of Grootberg, Boosmansbos Wilderness Area, Langeberg

Community									
1									
1.1		1.2							
		1.2.1		1.2.2		1.2.3		1.2.4	

Table 1. Cont. ...

Relevé number *	1*	1*	*	*	*	*	*	*	1
*66778992*2333366778889992*6678*855556* 1688*	1111*111122222777*	123337889*22336679 2							
*59089563*11346701470360120*2311*867894*13847*36890126*458905678356*457720599254*39286723 4									

Widespread species common to all Communities											
<i>Erica hispida</i> L.	.	++	++	5.23120	04441	1+	.4413.1	+ 5.1++43.223313	1.355444345352.412 2+2312 +.1+131 1		
<i>Elegia juncea</i> L.	.	1+++	+++	1+++11+1	112+	22	+++2.1121+2.	++2 +, 11	++0.12+ 1+ +2 21.1+++0 + + 1.11+ 121++		
<i>Chrysithrix capensis</i> L.	.	+2	+1	++++++1	+22	.	+	+	+	1.1+ ++.11+ 1+ +1 1.1+ ++11+ +.++111 + +	
<i>Pentastichis colorata</i> (Steud.) Stapf	.	2+++	R++	21	43312	+ 1	+1	1.1.+ + 3.+ 23	.	+ 2+ +, 2+ ++1 + .++1 22+0 0. 222 111	
<i>Tetraria flexuosa</i> (Thunb.) C.B. Cl.	.	1	+	1++++	131	1	414.	.	3	4. 41+++1.2 +1 1 10.5+4+2+1 1 1. 11+ 13	
<i>Thamnochortus cinereus</i> Linder	.	0		0+	11	1+	++ + +1	++++.	+	+	1 +.+++11 1+.++ 1
<i>Clusia alaternoides</i> L.	.	.	+	1+1+1+	++++	.	11.	++211.1+1 +. + + +.	++ +, R	1+ . 1++11+1	
<i>Ehrharta setacea</i> Nees ex Trin. subsp. scabra	.	++0+.	+	1	+	.	.	1	3+12 10+.32+++11+ 1+ .23+1 +	1.11 1+1+1	
<i>Blaeria coccinea</i> Klotzsch	.	+++113+22.	124++	+2+	1123++	1+.	+++1+.	+	.	01 . 2 . 2 +41++	
<i>Protea cynaroides</i> (L.) L.	.	20	+	1	1+ ++	1+	+++0	+0 +, +	.	1 1 11 0 . 00 . + 0 +	
<i>Epischoenus</i> cf. <i>adnatus</i> Levyns	.	++1	+	12	212	+	.	+	+	.	4 2+.
<i>Othonna quinqueidentata</i> Thunb.	.	++1+	1.	1+	+	1	+	.	+	+	++
<i>Blechnum tabulare</i> (Thunb.) Kuhn	.	1	.	0+	3.	1++	++ 1.
<i>Thesium carinatum</i> A. DC.	.	+	+	1	.	+	+++	.	.	.	++
<i>Penaea cneorum</i> Meerb. subsp. <i>ruscifolia</i> Dahlg.	.	1	.	.	+	.	1	+	1	1212220 .42+2+3	+ 1.1. R2 1+ . 3 1 3
<i>Tetraria thermalis</i> (L.) C.B. Cl.	.	1	.	.	+	.	.	+	.	1+	1+ 1 +.
<i>Hermas ciliata</i> L.f.	.	R	.	+	+++	+	.	.	.	R	R
<i>Syncarpha eximia</i> (L.) B. Nord.	.	0	0	.	+	R	.
<i>Indigofera concava</i> Harv.	.	+	+	.	+	++	+
<i>Lobelia pubescens</i> Dryand ex. Ait.var. <i>rotundifolia</i>	.	R	R	++	R	.
<i>Senecio ilicifolius</i> (L.) Thunb.	.	0	.	.	+	+	.	0	.	.	.
<i>Myrica kraussiana</i> Buching ex Meisn.	.	.	+	.	+	1.	.	+	.	+	.

community is given following the system for the Fynbos Biome proposed by Campbell *et al.* (1981).

Riparian communities were not sampled because they form narrow ribbons along streams, and are restricted to the streambanks. Typical dominants found in the non-forest riparian communities are: *Brachylaena neriifolia*, *Cunonia capensis*, *Elegia capensis*, *Empleurum uncapulare*, *Laurophyllus capensis*, *Rapanea melanophloeos*, *Todea barbara* and *Virgilia oroboides*.

Afromontane Forest

The forest patches in the BWA are typical Afromontane Forest. They are found in deep secluded gorges which are cool and moist. These forests are floristically all of one type, based on tree species composition. The Boosmansbos Forest tends to be much wetter than the other patches sampled, shown by the high cover-abundance of *Cyathea capensis* which favours such conditions. An apparently drier-phase forest patch (Relevé 122) is characterized by *Plectranthus fruticosus*. However, this observation is at variance with that of Muir (1929) who presented an early general account of the 'Langeberg Forest' at Riversdale. He maintained that *P. fruticosus* is strongly moisture demanding. McKenzie (1978) gives detailed descriptions of the Boosmansbos forests which he classified as the *Cunonia capensis*–*Platylophus trifolius* Subassociation. A number of 'variations' were distinguished within the Subassociation according to relative wetness and dryness. No additional information was recorded or change in the classification proposed based on the five 400 m² plots sampled in the present study. Structurally the forests are classified as Wet High Forest (w-HF) following Geldenhuys (1983). The canopy height varies from 20–30 m and the species recorded, with synoptic Braun-Blanquet values in parentheses, are as follows:

Trees: *Cunonia capensis* (5), *Halleria lucida* (4), *Hartogiella schinoides* (2), *Ilex mitis* (2), *Kiggelaria africana* (1), *Maytenus acuminata* (3), *Ocotea bullata* (4), *Olinia ventosa* (1), *Platylophus trifolius* (5), *Podocarpus latifolius* (2), *Pterocelastrus rostratus* (4), *Rapanea melanophloeos* (5), *Virgilia oroboides* (3).

Shrubs: *Diospyros whyteana* (1), *Plectranthus fruticosus* (1).

Ferns: *Asplenium adiantum-nigrum* (2), *Blechnum giganteum* (5), *B. punctulatum* (2), *B. tabulare* (2), *Cyathea capensis* (5), *Hymenophyllum tunbridgense* (2), *Rumohra adiantiformis* (1), *Todea barbara* (2).

Climbers: *Myrsiphyllum scandens* (3).

Herbs: *Epischoenus adnatus* (2), *Galium undulatum* (1), *Osmitopsis osmitoides* (1), *Peperomia retusa* var. *retusa* (1), *Schoenoxiphium lanceum* (5).

Epiphytes: *Elaphoglossum angustatum* (3), *Microsorium ensiforme* (4).

Geophytes: *Oxalis purpurea* (4).

Fynbos

The cool south slopes of the southern Langeberg are covered with physiognomically uniform plant communities over large areas. The slopes are moist and may be likened to an extensive seepage zone. Apart from Muir's (1929) classification the vegetation has been variously referred to as: Wet Sclerophyll Bush (Adamson 1938); Hygrophilous Macchia or Fynbos (Phillips 1931; Taylor 1978); False Macchia (Veld Type 70) by Acocks (1988); Wet Mountain Fynbos (Moll *et al.* 1984) and Wet Ericaceous Fynbos (Campbell 1985). The apparent uniformity is deceptive, however, with close examination showing that the vegetation can be subdivided on species composition into the eight shrubland communities described under 'A' below.

The most striking feature of the fynbos of the BWA is the clear division between the vegetation of the southern and northern sides of the mountain. *Erica hispidula*, a common dominant on the south slopes, is almost completely absent on the north slopes. Although a number of other species transgress the south-north boundary, for example *Leucadendron eucalyptifolium*, it is clear that a definite floristic distinction can be made between the shrublands on the south and north sides of the mountain. This distinction is reflected in the treatment of the data from the respective areas in separate syntaxonomic tables (Tables 1 & 2), where a hierarchical arrangement of communities is also presented.

Using the default options, TWINSpan clearly separated the mesic to dry shrublands north of Grootberg from the largely mesic to wet shrublands of the catchments south of Grootberg at Level 1. This is reflected in the treatment of the relevés in two separate phytosociological tables (Tables 1 & 2). Relevés 41 and 48, however, were included in Table 2, contrary to the TWINSpan classification.

In the mesic to wet *Erica hispidula* Shrublands, TWINSpan separates those relevés (except relevés 31, 33, 34, 36 & 37) which correspond with the *Erica hispidula*–*Spatalla nubicola* and the *Restio inconspicuus*–*Anthochortus crinalis* Shrublands in the BB classification from the remaining relevés which constitute the *Erica hispidula*–*Restio inconspicuus* Shrublands, at Level 2. Correlations between the two classifications from TWINSpan levels 3–6 are not good but show general similarities. Nine communities are identified using the BB classification method, whereas TWINSpan separates the relevés into 15 groups.

In the mesic to dry shrublands the distinction between the *Cannomois parviflora*–*Leucadendron eucalyptifolium* Shrublands and the *C. parviflora*–*Passerina obtusifolia* Shrublands (see below and Table 2) correlates directly with the separation indicated by the TWINSpan classification at Level 2. Correlation at lower levels (3–6) is not good. The BB classification results in four communities being identified, with further subdivision into 13 groups, as indicated by TWINSpan, considered to be too fine.

1. *Erica hispidula* Shrublands

Typical of the shrublands of the moist south-facing slopes of the southern Langeberg is the ubiquitous shrub *Erica hispidula*. This species is characteristic of much of the mesic to wet ericaceous fynbos of the mountains of the southwestern and southern Cape (Boucher 1978; Kruger 1979; Bond 1981; McDonald 1988), and is therefore used as a descriptor for these shrublands.

In BWA *E. hispidula* is widespread and links the south-slope shrublands floristically across physiognomic boundaries, with *Restio inconspicuus* playing a subordinate role. *R. inconspicuus* is absent only from the *Erica hispidula*–*Spatalla nubicola* Community, a feature attributed to the dense, waterlogged, humic substrate. *R. inconspicuus* in turn, however, links all the communities falling under the *Erica hispidula*–*Restio inconspicuus* Shrublands in the classification. These shrublands are equivalent to the Heathland, Mixed Sclerophyllous Scrub and Broad-sclerophyllous Scrub communities of Kruger (1979).

1.1 *Erica hispidula*–*Spatalla nubicola* Shrublands (A)

Differential species: *Spatalla nubicola*, *Helichrysium capense*.

Dominant species: *Anthochortus crinalis*, *Brunia alopecuroides*, *Platycaulos anceps*.

Structural formation: Closed Restioidland with Mid-high Mid-dense Shrubland Overstorey.

Relationships: *Brunia alopecuroides*–*Restio bifidus* Community (Kruger 1974); Subcommunity E2 of the *Erica*–*Penaea* Community (Glyphis *et al.* 1978); *Restio*–*Hypolaena* Subcommunity (H & I) (Laidler *et al.* 1978); Ericoid-Restioid Zone Fynbos (Taylor 1978); Low Narrow-sclerophyllous Heathland (Kruger 1979); *Simocheilus carneus*–*Restio anceps* Community (Bond 1981); Wet Mountain Fynbos (Moll *et al.* 1984); Ruitersberg Wet Ericaceous Fynbos (Campbell 1985); *Erica hispidula*–*Brunia alopecuroides* Shrublands (McDonald 1993a).

This community (Figure 4) is found on the steep, cool, moist southerly slopes of the BWA, mostly at altitudes above 1 200 m. The community is found in the 'mist zone' where low stratus cloud commonly occurs around the high ridges and peaks. Annual precipitation is estimated at 1 200 mm and insolation is generally low. There is a consequent accumulation of organic material. Champagne Form soils with a strongly acid organic horizon (pH 2.9 in 0.01 mol/l CaCl₂) as deep as 700 mm in some cases, form the substrate of this community.

These shrublands were sampled mainly on the south side of the ridge of Repeater Kop (Relevés 65, 69, 70, 78, 95 & 96), on Grootberg Summit (Relevé 123) and on the southwest side of the high ridge between Grootberg and Horingberg (Relevé 89).

Spatalla nubicola (Proteaceae) is endemic to this community whereas *Helichrysium capense*, the second differential species has a wider distribution, being found at other localities in the Langeberg. Presence of at least one of these species is necessary to determine this community. The dominant species *Brunia alopecuroides* gives these shrublands their characteristic 'brunioid' appearance. The *B. alopecuroides* shrubs seldom exceed 1.2 m in height and their closed canopy provides dense shade for the understorey restioid and ericoid elements. *Anthochortus crinalis* and *Platycaulos anceps* (Restionaceae) dominate the dense understorey stratum. Grasses are conspicuously lacking and are only represented by *Ehrharta setacea* subsp. *scabra*, a rare endemic in the fynbos biome (Gibbs Russell *et al.* 1990), in some stands.

A population of the rare *Spatalla colorata* was found in this community on the summit of Repeater Kop in close proximity to an undescribed endemic *Erica* species. These species apparently favour moist, high-altitude habitats with highly leached soils.

1.2 *Erica hispidula*–*Restio inconspicuus* Shrublands

This community comprises all the shrublands apart from the *Erica hispidula*–*Spatalla nubicola* Shrublands. *Restio inconspicuus* and several prominent species, namely



FIGURE 4. — *Erica hispidula*–*Spatalla nubicola* Shrublands on high altitude, steep south-facing slopes. Note the shrubby endemic *S. nubicola* next to the range rod.

Tetraria cuspidata, *Ehrharta dura*, *Erica melanthera* and others (see Table 1) are not found in the latter community. The soils on which the *Erica hispidula*–*Restio inconspicuus* Shrublands occur are generally either more freely drained, with less accumulation of organic material, or are derived from non-sandstone substrates.

1.2.1 *Restio inconspicuus*–*Anthochortus crinalis* Shrublands (B)

Differential species: none.

Dominant species: *Anthochortus crinalis*, *Erica hispidula*, *Ehrharta dura* and *Platycaulos anceps*.

Structural formation: Closed Graminoid Shrubland. Relationships: *Brunia alopecuroides*–*Restio bifidus* Community (Kruger (1974); Subcommunity E2 of the *Erica*–*Penaea* Community (Glyphis *et al.* 1978); *Restio*–*Hypolaena* Subcommunity (H & I) (Laidler *et al.* 1978); Ericoid–Restioid Zone Fynbos (Taylor 1978); Low Narrow-sclerophyllous Heathland (Kruger 1979);

Simocheilus carneus–*Restio anceps* Community (Bond 1981); Wet Mountain Fynbos (Moll *et al.* 1984); Ruitersberg Wet Ericaceous Fynbos (Campbell 1985); *Erica hispidula*–*Brunia alopecuroides* Shrublands (McDonald 1993a).

This community (Figure 5) has no differential species but shares many species with the *Erica hispidula*–*Spatalla nubicola* Shrublands (see Table 1); is characterized by absence of *Spatalla nubicola* and *Helichrysum capense*; and is found at altitudes higher than 1 000 m on east-, southeast-, south- and southwest-facing slopes. Sample quadrats were located at five general localities; on the upper south-facing slopes above Saagkuilkloof (Relevés 21 & 74), on the lower south- and southwest-facing slopes of Repeater Kop above Platbosrivierkloof (Relevés 34, 36, 37, 77, 80, 83, 120), on the south-facing slopes of the ridge west of Grootberg Peak (Relevés 60, 61 & 86), on the slopes southeast of Grootberg Peak overlooking Boosmansbos (Relevés 90 & 91) and on the east-facing slopes overlooking Boosmansbos (Relevés 31 & 33).



FIGURE 5. — *Restio inconspicuus*–*Anthochortus crinalis* Shrublands at altitudes above 1 000 m on southerly slopes.

Rainfall is between 1 000 and 1 200 mm annually, depending on altitude and aspect and the *Restio inconspicuus*–*Anthochortus crinalis* Shrublands are found mainly on highly leached Cartref Form soils (see SCWG 1991; Campbell 1983). Two samples (Relevé 90 & 91) were located on Champagne Form soils and show strong floristic affinity with the *Erica hispidula*–*Spatalla nubicola* Shrublands. However, these stands lack the differential species of the latter community.

Shrubs and graminoids are co-dominant, with the shrubs not exceeding 1 m. *Widdringtonia nodiflora* is present in some stands and is emergent up to 2 m. *Erica hispidula* and *Ehrharta dura* dominate with *Anthochortus crinalis* and *Platycaulos anceps* less conspicuous, forming part of the graminoid component.

A number of relevés (31, 36 & 92) do not have any of the differential species of the *Restio inconspicuus*–*Anthochortus crinalis* Community. They are regarded as samples from depauperate stands and are included here on the basis of dominant species and geographical position on the sample transect and in the landscape.

1.2.2 *Restio inconspicuus*–*Protea grandiceps* Shrubland (C)

Differential species: *Protea grandiceps*.

Dominant species: *Erica hispidula*, *Tetraria flexuosa*, *Tetraria bromoides*.

Structural formation: Closed Graminoid Shrubland.

Relationships: *Tetraria bromoides*–*Erica plukenetii* Community (Kruger 1974); *Protea*–*Tetraria* Dry Short Fynbos (Boucher 1978); Wet Mountain Fynbos (Moll *et al.* 1984); Boesmansbos Azonal Restioid Fynbos (Campbell 1985); *Pentaschistis malouinensis*–*Tetraria bromoides* Shrubland (McDonald 1993a).

This community (Figure 6) is localized on the south-facing lower to mid-slopes of the ridge west of Grootberg, overlooking the Helderfontein Valley, at 1 180–1 295 m altitude. This locality lies more or less on the contact between the Cedarberg Formation and the Nardouw Subgroup. The soils are mainly Cartref Form, where

sandstone is the parent rock (Relevés 62, 63 & 71) and Clovelly Form, where shale is the parent rock (Relevé 81).

Mean annual precipitation at this locality is 1 000–1 100 mm and the soils are well drained but slightly more nutrient-rich than soils derived from Peninsula Formation sandstone (G.N. Schafer pers. comm.). The poleward aspect permits lower insolation, and *P. grandiceps* apparently favours the cooler slopes and richer soils.

This community is structurally similar to those of most other parts of the high-altitude slopes. *E. hispidula* dominates the shrub component with *P. grandiceps* having notable cover-abundance in only two of the four plots sampled (Relevés 62 & 63). Sedges such as *Tetraria flexuosa* and *Tetraria bromoides* dominate the herbaceous component. Close affinity exists between the *Restio inconspicuus*–*Protea grandiceps* Shrubland and the *Restio inconspicuus*–*Protea aurea* Shrubland, with these two communities sharing species not common to other communities (see Table 1).

1.2.3 *Restio inconspicuus*–*Protea aurea* subsp. *aurea* Shrublands (D)

Differential species: *Protea aurea* subsp. *aurea*.

Dominant species: *Protea aurea* subsp. *aurea*.

Structural formation: Mid-high to Tall Proteoid Shrubland with a Closed Graminoid Shrubland Understorey.

Relationships: *Tetraria bromoides*–*Erica plukenetii* Community (Kruger 1974); *Protea*–*Tetraria* Dry Short Fynbos (Boucher 1978); *Protea aurea*–*Pteridium aquilinum* Community (Bond 1981); Wet Mountain Fynbos (Moll *et al.* 1984); Boesmansbos Azonal Restioid Fynbos (Campbell 1985); *Pentaschistis malouinensis*–*Tetraria bromoides* Shrubland (McDonald 1993a).

In BWA this community (Figure 7) occurs at altitudes above 1 100 m on the Cedarberg shaleband, near Helderfontein. The shales of the Cedarberg Formation weather to produce fine-grained, clay-rich yellow-brown Clovelly Form soils, and *Protea aurea* is found almost exclusively on these soils. This correlation is found throughout the



FIGURE 6. — *Restio inconspicuus*–*Protea grandiceps* Shrubland localized on the south-facing slopes west of Grootberg.



FIGURE 7.—*Restio inconspicuus*—*Protea aurea* subsp. *aurea* Shrublands found on the Cedarberg Formation shale near Helderfontein.

Langeberg, regardless of the altitude at which the shale-band is exposed. *P. aurea* can therefore be used as a marker indicating the exposure of the Cedarberg Formation in the highly folded strata of the Langeberg.

Sample plots were located between Helderfontein and Boosmansbos (Relevés 56, 57, 58 & 59) on northeast-, southeast- and southwest-facing slopes. Two plots (Relevés 64 & 88) were also located on the lower south- and southwest-facing slopes of the ridge west of Grootberg, above the watershed between the Helderfontein and Moeras River Valleys. Relevé 88 represents a transitional situation between Communities 2.2 and 2.3 but since *P. aurea* has a relatively high BB value (3), and since the soil is Clovelly Form, it is included in the *Restio inconspicuus*—*Protea aurea* Shrublands.

1.2.4 *Restio inconspicuus*—*Hypodiscus aristatus* Shrublands 'Typicum' (I)

Differential species: none.

Dominant species: *H. aristatus*, *R. inconspicuus*, *Ehrharta dura*.

Structural formation: Closed Graminoid Shrubland.

Relationships: *Tetralia thermalis*—*Hypodiscus aristatus* Community (Kruger 1974); Mixed ericoid and restioid fynbos of the xeric slopes (Boucher 1978); *Leptocarpus membranaceus*—*Hypodiscus aristatus* Community (McKenzie *et al.* 1977); Subcommunities B & C of the *Erica*—*Penaea* Community (Glyphis *et al.* 1978); *Tetralia thermalis* Bergpalmietveld (Taylor 1978); Low ericoid open-heath or open graminoid-heath (Kruger 1979); *Erica viridescens*—*Hypodiscus aristatus* Community (Bond 1981); Mesic Mountain Fynbos (Moll *et al.* 1984); Nuweberg Mesic Ericaceous Fynbos (Campbell 1985); *Erica hispidula*—*Hypodiscus aristatus* Shrublands (McDonald 1993a).

The relevés grouped here (23, 29, 32, 38, 66, 67, 72, 93, 124) represent the 'typicum' of the *Restio inconspicuus*—*Hypodiscus aristatus* Shrublands (Figure 8). This 'typicum' or 'background community' has no floristic

elements which allow subdivision into lower-ranking communities; as such it is regarded as depauperate.

These shrublands occur on shallow (0.1–0.15 m), well-drained and highly leached Cartref and Houwhoek Form soils at altitudes from 1 000–1 500 m. Parent rock is mainly Peninsula Formation sandstone with Nardouw Subgroup sandstone found in plots 92 and 124. Aspect is generally north- and northwest-facing, with two exceptions, plots 29 and 30 which face south and southeast. Surface rock cover ranges between five and 75 %; boulders were found in all plots and exposed bedrock in more than 50 %. Although rainfall probably exceeds 1 000 mm per annum, high insolation coupled with good drainage is most likely the reason for the depauperate nature and low stature of the community.

Shrubs such as *Erica hispidula* and *Penaea cneorum* subsp. *ruscifolia* are emergent up to 1.2 m but grasses (*Ehrharta dura*, *Pentastichis colorata*), restios (*Hypodiscus aristatus*, *Restio inconspicuus*) and sedges (*Tetralia* spp.) dominate the low stratum (<0.5 m). Although strongly similar structurally and in species composition to the *Restio inconspicuus*—*Anthochortus crinalis* Shrublands, the *Restio inconspicuus*—*Hypodiscus aristatus* Shrublands have *Hypodiscus aristatus* dominant, whereas it is absent from the former community. Apparently north versus south aspects and relative wetness-dryness account for the change in species dominance and consequent distinction between these two communities.

1.2.4.1 *Hypodiscus aristatus*—*Leucadendron eucalyptifolium* Shrublands (E)

Differential species: none.

Dominant species: *Leucadendron eucalyptifolium*.

Structural formation: Mid-high to Tall, Mid-dense to Closed Proteoid Shrublands.

Relationships: *Berzelia*—*Leucadendron* Moist Tall Fynbos (Boucher 1978); Mixed Sclerophyllous Scrub (Kruger 1979); *Protea neriifolia*—*Leucadendron eucalyptifolium*—*Erica triceps* Community (Bond 1981); Mesic Mountain



FIGURE 8—*Restio inconspicuus*–*Hypodiscus aristatus* Shrublands found on shallow, well-drained, highly leached sandstone soils at altitudes from 1 000–1 500 m.

Fynbos (Moll *et al.* 1984); Robinson Mesic Proteoid Fynbos (Campbell 1985).

Leucadendron eucalyptifolium is a tall proteoid shrub ubiquitous on the Langeberg. It is found at localities on south and north sides of the range. In the BWA, *L. eucalyptifolium* occurs in the Mesic Proteoid Fynbos north of Grootberg as well as at the southern end of the sample transect, on the shaleband at Helderfontein and at the head of the Moeras River Valley. Where *L. eucalyptifolium* occurs with *Protea aurea* it is found on Clovelly Form soils but in the community described here (Figure 9) the soils are either of Oakleaf or Cartref Forms.

L. eucalyptifolium shrubs up to 2.5 m high dominate the community and it is the only species found in all relevés. Relevés 1 and 13 show marked floristic affinities with the *Restio inconspicuus*–*Protea aurea* Shrublands, whereas the remaining three relevés do not. This is

attributed to the nature of this community to transgress soil types.

Plots 1, 13 and 84 were situated in localized stands of the *Hypodiscus aristatus*–*Leucadendron eucalyptifolium* Shrublands on Oakleaf Form soils derived from conglomerates of the Enon Formation, detailed above. The soils are loamy with pH 4.3 (in 0.01 mol/l CaCl₂) in the A-horizon increasing to pH 5.3 in the B-horizon. Aspect is west to southwest at altitudes of just less than 400 m. Mean annual precipitation at these sites is estimated at 800–900 mm.

In contrast, plots 68 and 87 were located in extensive stands of the community at altitudes 1 200–1 340 m on slopes with a northwesterly aspect. Parent rock is Peninsula Formation sandstone with Cartref Form soils. These soils are somewhat more leached and acid (pH 3.2 in 0.01 mol/l CaCl₂) in the A- and E-horizons than the loamy



FIGURE 9.—*Hypodiscus aristatus*–*Leucadendron eucalyptifolium* Shrublands on a northwest-facing slope on sandstone soil west of Helderfontein.



FIGURE 10.—A dense stand of the *Berzelia intermedia*–*Erica melanthera* Shrublands on the lower south slopes of BWA.

Oakleaf Form soils. Mean annual precipitation is estimated at 1 000 mm.

1.2.4.2 *Hypodiscus aristatus*–*Berzelia intermedia* Shrublands

The *Hypodiscus aristatus*–*Berzelia intermedia* Shrublands comprise two communities, the *Berzelia intermedia*–*Erica melanthera* Shrublands and the *Berzelia intermedia*–*Erica blenna* Shrublands. These shrublands occur at altitudes not higher than 875 m (330–860 m) on the south slopes of the BWA, and give these slopes their characteristic ericoid-brunioid (fine-leaved) appearance. The parent rock is Peninsula Formation sandstone throughout. *Berzelia intermedia* is conspicuously present throughout these shrublands.

1.2.4.2.1 *Berzelia intermedia*–*Erica melanthera* Shrublands (F)

Differential species: *Lobelia coronopifolia*, *Pentaschistis* sp.

Dominant species: *Erica hispidula*, *Erica melanthera*, *Hypodiscus aristatus*, *Penaea cneorum* subsp. *ruscifolia*, *Tetraria cuspidata*.

Structural formation: structure of this community varies between a Low Closed Ericoid Shrubland and a Closed Graminoid Shrubland depending on the density and cover of the shrub component.

Relationships: Fynbos of the ericoid–restioid zone (Taylor 1978); Low Ericoid Heathland (Kruger 1979); *Erica arachnoidea*–*Pentameris dregeana* Community (Outeniqua Mountains) and the *Erica petraea*–*Erica nervata* and *Protea punctata*–*Erica melanthera*, *E. andraei* Communities (Swartberg) (Bond 1981); Mesic Ericaceous Fynbos (Moll *et al.*); Landdros Mesic Ericaceous Fynbos (Campbell 1985).

The dominant species, *Erica melanthera* is characteristic of this community (Figure 10). Dense stands of this erica are visible from a long distance, flowering on the lower slopes of the Langeberg in spring (Muir 1929; McDonald pers. obs.). Since the *Hypodiscus aristatus*–*Erica melan-*

thera Shrublands are poorly defined by inconspicuous differential species and because *Erica melanthera* is easily identified, it was chosen for the naming of this community. *Erica hispidula* is less dominant than *Erica melanthera* but is nevertheless well represented, as is *Penaea cneorum* subsp. *ruscifolia*. The dominant graminoids are *Hypodiscus aristatus* (Restionaceae), *Tetraria cuspidata* (Cyperaceae) and *Ehrharta setacea* subsp. *scabra* (Poaceae). Together with other restios, sedges and grasses such as *Pentaschistis* spp. they constitute the co-dominant graminoid component.

The altitude at which these shrublands are found ranges from 330–625 m with a mean of 490 m. The soils are shallow (100–150 mm), acid (pH 3.2 in 0.01 mol/l CaCl₂, A-horizon) Cartref Form throughout the community. Mean annual precipitation is estimated at 900–1 000 mm. Typically these shrublands occur on gentle slopes with a mean gradient of 10° (5°–21°) with extremely variable amounts of exposed rock (0–75% cover).

1.2.4.2.2 *Berzelia intermedia*–*Erica blenna* var. *blenna* Shrublands (G)

Differential species: none.

Dominant species: *Berzelia intermedia*, *Erica blenna* var. *blenna*, *Erica hispidula*, *Psoralea pinnata*, *Widdringtonia nodiflora*.

Structural formation: the community is classified as a Low to Mid-high Closed Shrubland with a Mid-dense to Closed Graminoid Understorey.

Relationships: *Berzelia lanuginosa*–*Osmitopsis asteriscoides* Community (Werger *et al.* 1972); *Erica*–*Osmitopsis* Seepage Fynbos and *Chondropetalum*–*Berzelia* Upper Hygic Fynbos (Boucher 1978); Hygrophilous Fynbos (Taylor 1978); Variation I of the *Restio*–*Hypolaena* Subcommunity (Laidler *et al.* 1978); Mixed Sclerophyllous Scrub (Kruger 1979); *Berzelia*–*Osmitopsis* Seepage Fynbos on permanent seeps (Taylor 1984); Wet Mountain Fynbos (Moll *et al.* 1984); Keurbos Wet Ericaceous Fynbos (Campbell 1985); *Berzelia lanuginosa*–*Merxmüllera cincta* Tall Closed Shrubland (McDonald 1988); *Erica hispidula*–*Berzelia intermedia* Shrublands (McDonald 1993a).

As noted above, *Berzelia intermedia* is characteristic of the *Hypodiscus aristatus*–*Berzelia intermedia* Shrublands (1.2.4.2). It is most dominant in the *Berzelia intermedia*–*Erica blenna* Shrublands (Figure 11). *Erica hispidula* also attains its highest degree of dominance in this community. *Erica melanthera* is present but much less evident than in the *Berzelia intermedia*–*Erica melanthera* Shrublands. *Widdringtonia nodiflora* is a conspicuous emergent shrub (up to 4 m) in most stands, whereas it is almost totally absent from the latter community. *E. blenna* var. *blenna* is endemic to the Langeberg and is restricted to the Swellendam–Heidelberg part of the range. It is used in the name of the *Berzelia intermedia*–*Erica blenna* Shrublands because it has its strongest expression here and the community is otherwise poorly defined. *Psoralea pinnata* is also found commonly here but it has a wider tolerance, occurring in other communities as well (Table 1). Two other species of particular note which occur in this community are the rare Langeberg endemics *Linconia alopecuroides* L. (Bruniaceae) and *Carpacoce gigantea* Puff (Rubiaceae).

This community is also found on highly leached, low pH, shallow (<300 mm) soils of Cartref and Houwhoek Forms. Rock cover is mostly 2% or less except in plots 18 (10%) and 76 (25%). The slopes where these shrublands are located vary in aspect from east- to south-facing; one sample plot (73) was located on a west-north-west-facing slope. The mean gradient of the slopes is 19° (10°–33°). Altitudinal range of the community is from 500–850 m with a mean of 670 m. The *Berzelia intermedia*–*Erica blenna* Shrublands thus occupy the zone of higher, steeper slopes than the *Berzelia intermedia*–*Erica melanthera* Shrublands but occur below the zone occupied by the *Restio inconspicuus*–*Anthochortus crinalis* Shrublands (1.2.1) and *Restio inconspicuus*–*Hypodiscus aristatus* Shrublands (1.2.4). Mean annual precipitation is estimated at 1 000–1 100 mm.

Structurally the *Berzelia intermedia*–*Erica blenna* Shrublands are variable. In general the upper shrub stratum does not exceed 1.5 m in height. The exceptions are where *Berzelia intermedia* is dominant and reaches 2.5–3.0 m in height with a high projected canopy cover (Relevés 26 &

76) or where *Widdringtonia nodiflora* reaches 3–4 m and exceeds 10% projected canopy cover (Relevés 20 & 25).

1.2.4.3 *Hypodiscus aristatus*–*Erica versicolor* Shrublands (H)

Differential species: *Erica versicolor*, *Centella virgata* and *Tetraria involucreata*.

Dominant species: *Erica versicolor*, *Erica hispidula*, *Erica melanthera*, *Hypodiscus aristatus* and *Tetraria flexuosa*.

Structural formation: Closed Graminoid Shrubland or a Closed Herbland with a Mid-high Mid-dense Ericoid Shrubland Overstorey.

Relationships: Mesic Mountain Fynbos (Moll *et al.* 1984); *Hypodiscus aristatus*–*Erica versicolor* Shrublands (McDonald 1993a).

This community (Figure 12) is typically found on rocky sandstone outcrops on northwest-, north- and northeast-facing slopes, but on the south side of the range (i.e. south of Grootberg).

Soil development on the rocky outcrops where the *Hypodiscus aristatus*–*Erica versicolor* Community is found is poor, consisting of accumulations of sand and organic material in shallow (100 mm deep) pockets amongst the rocks. These lithosols are therefore regarded as poorly developed Mispah Form soils.

Erica versicolor has the habit of favouring almost any well-drained rocky situation and the *Hypodiscus aristatus*–*Erica versicolor* Shrubland Community is usually interspersed amongst other more uniformly distributed communities, forming a mosaic with the latter from low to high altitudes (400–1 200 m). The community is characterized as much by presence of *Erica versicolor* as by marked absence of a number of widely distributed species, e.g. *Cyclopia sessiliflora*, *Drosera aliceae*, *Tetraria compressa* and *Gnidia oppositifolia*, which prefer habitats where the soils are deeper and less readily drained.

The stature of *Erica versicolor* ranges from low (<1 m) to mid-high (1–2 m) and therefore the structural form



FIGURE 11.—*Berzelia intermedia*–*Erica blenna* Shrublands which occur on highly leached acid sandstone soils at altitudes from 1 000–1 100 m mainly on wet south-facing slopes.



FIGURE 12. —*Hypodiscus aristatus*–*Erica versicolor* Shrublands found on rocky sandstone outcrops on the south side of the Langeberg in BWA.

of the *Hypodiscus aristatus*–*Erica versicolor* Community varies between the two forms stated above.

2. *Cannomois parviflora* Shrublands

Species with distribution common to all plant communities and with high cover-abundance are not a feature of the vegetation on the north slopes of the Langeberg in the Boosmansbos Wilderness Area. Broad-scale characterization of the plant communities occurring in this area is therefore not simple. *Cannomois parviflora* has been chosen as the 'base' species equivalent to *Erica hispidula* on the south slopes, since it is readily identifiable and found in all the communities in question (Table 2). Campbell (1985) notes that *Cannomois parviflora* (his *Elegia parviflora*) is common as a dominant in Mesic Restioid Fynbos and is also a feature of Dry Restioid Fynbos and Dry Proteoid Fynbos. This supports the use of this species in the nomenclature of the shrublands described here.

The *Cannomois parviflora* Shrublands are found on soils derived exclusively from sandstone of the Nardouw Subgroup. The communities described may or may not reflect the respective geological formations within the Nardouw Subgroup but distinctions in geological formation were not recorded and correlations between plant communities and geological formations are therefore not possible here. Four communities are identified and described, two as subdivisions of the *Cannomois parviflora*–*Leucadendron eucalyptifolium* Shrublands and two as subdivisions of the *Cannomois parviflora*–*Passerina obtusifolia* Shrublands.

2.1 *Cannomois parviflora*–*Leucadendron eucalyptifolium* Shrublands

Northeast of Grootberg is a shallow intermontane valley forming part of the catchment of Brandrivier. There are also a number of east-trending rocky ridges, the highest of which is named Deception Ridge in this study. Altitude diminishes eastwards towards Brandrivier. The valley has a mesic to dry climate compared with the wet south slopes and the arid north slopes adjacent to the Little Karoo.

The soils are mainly accumulations of well-drained sand resulting in Clovelly Form soils. The ridges have a somewhat more xeric climate with shallow well-drained lithosols usually of Glenrosa Form.

This community is found in the above-mentioned intermontane valley and on the ridges but not on the arid north-facing slopes of Deception Ridge. They are locally extensive and are divided into two communities, the *Leucadendron eucalyptifolium*–*Protea lorifolia* Shrublands and the *Leucadendron eucalyptifolium*–*Staberoha cernua* Shrublands which are characterized by high cover-abundance of *Leucadendron eucalyptifolium*, *Protea repens* and *Tetradlea bromoides*. The presence of *Leucadendron eucalyptifolium* indicates a close relationship between these shrublands and the *Hypodiscus aristatus*–*Leucadendron eucalyptifolium* Shrublands (1.2.4.1) described above. Their overall species composition and habitat differ, however, and they are therefore treated as separate communities. The tall shrub *Protea eximia* occurs sporadically throughout the *Cannomois parviflora*–*Leucadendron eucalyptifolium* Shrublands and as a dominant in the *Leucadendron eucalyptifolium*–*Staberoha cernua* Shrublands described below.

The *Leucadendron eucalyptifolium*–*Protea lorifolia* Shrublands are found on the rocky ridges north of Grootberg, forming a mosaic with the *Leucadendron eucalyptifolium*–*Staberoha cernua* Shrublands which occur in bottomland situations. Physiognomically the former community differs very little from the latter. Both have a Mid-dense to Closed Graminoid stratum with Mid-high to Tall, Open to Mid-dense to Proteoid Shrub Overstorey. It is therefore difficult to distinguish these communities on the basis of structure.

2.1.1 *Leucadendron eucalyptifolium*–*Protea lorifolia* Shrublands (J)

Differential species: *Agathosma cerefolium*, *Erica versicolor*, *Indigofera pappi*, *Lightfootia tenella*, *Metalasia gnaphalodes*, *Protea lorifolia*, *Stoebe aethiopica*, *Stoebe saxatilis*, *Ursinia nudicaulis*.



FIGURE 13. —*Leucadendron eucalyptifolium*–*Protea lorifolia* Shrublands found on the ridges north of Grootberg, showing the proteoid shrub overstorey with *P. lorifolia* in the left foreground.

Dominant species: *L. eucalyptifolium*, *Elegia filacea*, *Protea repens*, *Tetraria bromoides*, *Thoracosperma galpinii*.

Structural formation: Mid-dense to Closed Graminoid Shrubland with a Mid-high to Tall, Open to Mid-dense Proteoid Shrubland Overstorey.

Relationships: Proteoid Zone Fynbos (Taylor 1978); Broad-sclerophyllous Scrub or Open-scrub (Kruger 1979); *Elegia galpinii*–*Metalasia pulcherrima* Community (Outeniqua Mountains) and *Protea repens*–*Protea lorifolia*–*Hypodiscus striatus* Community (Swartberg) (Bond (1981); Mesic Mountain Fynbos (Moll *et al.* 1984); Thomas Dry Proteoid Fynbos (Campbell 1985).

This community (Figure 13) is found on the ridges north of Grootberg. It is best expressed on Deception Ridge where there are terraces of shallow sandy loam Clovelly Form soil (Relevés 24, 52, 53, 55, 97, 98, 99, 100) and more poorly expressed where Glenrosa Form soils occur (Relevés 47, 49, 102, 113).

Mean annual precipitation is estimated at 600–700 mm. The general aspect is northeasterly but varies at local sites from north through east to south. Although most sites are well exposed and in many respects equivalent, local site aspect apparently plays some role in determining the distribution of the community. This is currently being investigated (McDonald, unpublished).

This community is structurally variable. The lowest stratum is always dominant, with sedges, restios and ericoid shrubs in more or less equal proportions. The upper stratum consists mainly of proteoid shrubs. The broad-leaved *P. lorifolia* is particularly characteristic and apart from some transgression into the *Leucadendron eucalyptifolium*–*Staberoha cernua* Shrubland (see Table 2), the dominant *Protea repens* could be viewed as characteristic of this community as well.

The presence of *Erica versicolor* in the *Leucadendron eucalyptifolium*–*Protea lorifolia* Shrublands indicates some affinity between this community and the *Hypodiscus aristatus*–*Erica versicolor* Shrublands described above. However, *E. versicolor* tends to be a ubiquist on rocky outcrops if the moisture régime is high enough and the limited presence of the species in this community is thought to indicate the limit of its range on the south-north gradient. *Erica barrydalensis* H. Bol., a rare endemic species, with similar rocky habitat preferences to *E. versicolor*, was recorded on Deception Ridge (McDonald & Oliver 1987) and may replace *E. versicolor* since it apparently tolerates xeric conditions more readily.

2.1.2 *Leucadendron eucalyptifolium*–*Staberoha cernua* Shrublands (K)

Differential species: *Cyphia zeyheriana*, *Erica cerinthoides*, *Helichrysum rotundifolium*, *Lachnaea penicillata*, *Staberoha cernua*.

Dominant species: *Leucadendron eucalyptifolium*, *Protea eximia*, *Tetraria bromoides*, *Elegia filacea*.

Structural formation: Mid-dense to Closed Graminoid Shrubland with a Mid-high to Tall, Open to Mid-dense Proteoid Shrubland Overstorey.

Relationships: as for 2.1.1 above.

The differential species of this community (Figure 14) are not well-represented. It could be argued therefore that distinction between the *Leucadendron eucalyptifolium*–*Protea lorifolia* Shrublands and the *Leucadendron eucalyptifolium*–*Staberoha cernua* Shrublands is tenuous. However, the proteoid stratum of the latter community is dominated by *Protea eximia* and *Leucadendron eucalyptifolium* with *Protea repens* almost absent. In the *Leucadendron eucalyptifolium*–*Protea lorifolia* Shrublands, the opposite is true with *P. eximia* poorly represented and *L. eucalyptifolium* and *Protea repens* co-dominant. Absence of a number of species such as *Anomalanthus* sp., *Ficinia lacinata*, *Hypodiscus argenteus*, *Hypodiscus striatus*, *Phyllica mairei*, *Relhania calycina* subsp. *apiculata* and *Stoebe microphylla* from the *Leucadendron eucalyptifolium*–*Staberoha cernua* Shrubland reinforces the distinction as well (see Table 2).

Structurally the *Leucadendron eucalyptifolium*–*Staberoha cernua* Shrublands are similar to the *Leucadendron eucalyptifolium*–*Protea lorifolia* Shrublands. The lower stratum is marginally more graminoid and the upper proteoid stratum more uniformly mid-dense. Other distinctions are negligible.

The *Leucadendron eucalyptifolium*–*Staberoha cernua* Shrublands are found mainly in bottomland situations with south- and southeast-facing aspects. One sample (Relevé 48) was on a 30° slope but mostly the community occurs



FIGURE 14 — *Leucadendron euca-lyptifolium*–*Staberoha cernua* Shrublands in bottomland situations. Note the dense graminoid understorey with *Protea eximia* dominant in the proteoid shrub stratum.

where there is little or no relief apart from a shallow gradient eastwards towards Brandrivier. The soils have resulted from accumulation of sand and are all distinctly yellow and of the Clovelly Form. A typical pH 4.6 increasing to pH 4.8 (in 0.01 mol/l CaCl_2) was measured for samples from the A- and B-horizons respectively of soil at Relevé 105.

2.2. *Cannomois parviflora*–*Passerina obtusifolia* Shrublands

This community is found on the exposed north-facing slopes of Deception Ridge below an altitude of 1 000 m and on the mesa-like sandstone plateaux above the contact with the Bokkeveld Formation shales of the Little Karoo. This is the most arid aspect of the transect, with high incoming radiation and rainfall ranging between 300–600 mm p.a. Two communities are described, the first being the *Cannomois parviflora*–*Passerina obtusifolia* 'Typicum' and the second the *Passerina obtusifolia*–*Leucospermum calligerum* Shrublands.

Passerina obtusifolia is a widespread species found on sandstone soils on the dry aspects of the mountains from Clanwilliam Division in the west to Grahamstown in the east (Thoday 1924). Occurrence of this species on the lower north slopes of the Langeberg clearly places the *Cannomois parviflora*–*Passerina obtusifolia* Shrublands within the context of Dry Mountain Fynbos (Moll *et al.* 1984).

The species shared between the two communities show definite affinities with Karroid vegetation; succulents in the genera *Adromischus*, *Crassula*, *Machairophyllum* and *Ruschia* indicate the transition from fynbos to Succulent Karoo. The endemic *Leucospermum erubescens* is found in these shrublands but was not encountered in any of the sample plots. Its distribution appears to be erratic on the north slopes of the Langeberg from Witbooisrivier to Garcia's Pass.

2.2.1 *Passerina obtusifolia*–*Leucospermum calligerum* Shrublands (L)

Differential species: *Elytropappus cyathiformis*, *Leucospermum calligerum*, *Lobostemon decorus*, *Muraltia heisteria*, *Paranomus spathulatus*, *Serruria balanoccephala*, *Thamnochortus karoocica*, *Thesium subnudum*.

Dominant species: *Leucospermum calligerum*, *Metalia densa*, *Passerina obtusifolia*, *Pentastichis eriostoma*, *Serruria balanoccephala*.

Structural formation: Mid-high Mid-dense Graminoid Shrublands.

Relationships: Arid Fynbos (Taylor 1978); Arid Fynbos (Kruger 1979); *Phyllica axillaris*–*Felicia filifolia* Community (Outeniqua Mountains) and *Passerina obtusifolia*–*Felicia filifolia*–*Pentastichis eriostoma* Community (Swartberg) (Bond 1981); Dry Mountain Fynbos (Moll *et al.* 1984); Sebrafontein Dry Asteraceous Fynbos (Campbell 1985).

This community (Figure 15) is found on the lower north-facing slopes above Witbooisrivier at altitudes from 485–745 m. The habitat is not much different from that of the *Cannomois parviflora*–*Passerina obtusifolia* 'Typicum' except that the mean gradient of the sample sites is 8° (6°–22°). With this difference in mean gradient, changes in drainage and other subtle factors may account for the development of this community.

Leucospermum calligerum is a widely distributed proteoid species on the arid aspect of the fynbos of the northwestern and western mountains (Lokenberg and Gifberg) and on the dry north slopes of the Langeberg to the Gouritz River in the east (Rourke 1972). It therefore links this community with the widely distributed Arid Fynbos (*sensu* Taylor 1978; Kruger 1979), Dry Mountain Fynbos (Moll *et al.* 1984) or Dry Asteraceous Fynbos (Campbell 1985). At a local scale, however, endemic species such as *Paranomus spathulatus* and *Serruria balanoccephala* Rourke ined., characterize the Dry Moun-

tain Fynbos of the north slopes of the Langeberg; a more refined definition of this community may be possible with more extensive sampling.

2.2.2 *Cannomois parviflora*–*Passerina obtusifolia* Shrublands 'Typicum' (M)

Differential species: none.

Dominant species: *Hypodiscus striatus*, *Passerina obtusifolia*, *Pentaschistis eriostoma*.

Structural formation: Open Graminoid Shrubland with ericoid shrubs emergent to 2 m.

Relationships: As for 2.2.1 above and *Leucadendron eucahyptifolium*–*Hypodiscus argenteus* Shrubland (McDonald 1993a) in part.

Four relevés, 45, 46, 50 & 51, represent this community. The first two sample plots were located on the lower north slopes above Klein Witbooisrivier at 594 m a.s.l. The soils are of Mispah Form reflecting poor soil development. Relevés 50 & 51 are at 792 and 914 m a.s.l. respectively on the rocky north-facing slopes of Deception Ridge. The soils at these sites are classified as Glenrosa Form. The mean gradient of the sites is 24° and rock cover is not less than 95% at any of the sites.

All the species in the *Cannomois parviflora*–*Passerina obtusifolia* Shrublands are shared with other communities. The xeric conditions at the above sites limit the survival of many plant species and the community consequently lacks species requiring more favourable conditions.

DISCUSSION AND CONCLUSIONS

Much debate has surrounded the classification of the fynbos vegetation of the Cape Floristic Region. Various methods have been used in attempts to classify the floristically complex vegetation into ecologically meaningful yet 'practical' units interpretable by scientist and manager alike.

Two approaches to the classification of the fynbos of mountain ecosystems in the Cape have been used since

the early 1970's: (i) the floristic approach and (ii) the structural approach. The floristic approach has been based mainly on the methodology of the Zürich-Montpellier school of phytosociology (Mueller-Dombois & Ellenberg 1974; Werger 1974). However, one of the problems facing phytosociologists in the fynbos of the Cape mountains is the great diversity of habitats and attendant high diversity of plant taxa (Werger *et al.* 1972). Floristic techniques have demanded high skills in identifying plants in the field, for example according to Bond (1981), 'high species turnover along geographic gradients places high demands on the ecologist's ability in field taxonomy for limited returns in ecological understanding. ... This reduces the generality and usefulness of a formal phytosociological approach to parochial studies in small areas.' Campbell (1986a & b) affirmed Bond's statement and severely criticised floristic techniques. However, despite this major area of difficulty the mosaic of small, localized studies that have been done have been useful in generating an overall picture of at least the broad fynbos communities present in the Cape mountains.

On the Langeberg, Muir's (1929) early descriptions, Taylor's (1955) documentation of Grootvadersbosch Forest, McKenzie's (1978) study of the forests and Campbell's (1983, 1985, 1986a) structural classification were the only studies of the vegetation prior to the present study. Campbell (*loc. cit.*) placed 21 samples in BWA on his 'Langeberg Transect' which he classified into six subseries (i) Azonal and (ii) Mesic Restioid Fynbos, (iii) Mesic and (iv) Wet Ericaceous Fynbos and (v) Mesic and (vi) Dry Proteoid Fynbos; 12 types were described. However, although Campbell's (1985) classification provides a comprehensive typology of Cape mountain vegetation (Cowling & Holmes 1992) it lacks floristic information found in phytosociological studies, which Bond *et al.* (1992) and Cowling *et al.* (1992) found appropriate for testing ecological and phytogeographical hypotheses. The application of the Braun-Blanquet method in this study was time-consuming but ultimately yielded an acceptable classification of the fynbos plant communities of the BWA. The classification is ecologically meaningful and easily interpretable if the user is familiar with the character species which form only a small proportion of the diverse



FIGURE 15. —*Passerina obtusifolia*–*Leucospermum calligerum* Shrublands on the dry lower north-facing slopes at Witbooisrivier, bordering the Little Karoo.

flora. The floristic data assembled in this study also provide a basis not only for description and hierarchical classification of fynbos plant communities but also for biogeographical studies.

The fynbos of mountain catchments of the southern Langeberg accords with Taylor's (1978) broad zonation classification of Cape mountain vegetation. In BWA, however, complex environmental gradients exist from the mesic lower south slopes through a number of fault valleys to wet high-altitude slopes and exposed peaks and ridges and then to the mesic to dry shallow valleys and ridges and very dry, exposed north slopes. This has profound local effects on the distribution of vegetation associations.

Correlation between environment and plant communities enhances the descriptive and predictive value of any phytosociological classification (Campbell 1983; McDonald 1987; Deall *et al.* 1989). Such correlations have necessarily been superficially described in this paper. Therefore, attempts to explain the gradients underlying the distribution of the communities described here will be presented in a later paper (McDonald, unpublished) where data from two additional sample transects will be available.

In attempting to show relationships between the communities described in this paper and those described by other workers in Mountain Fynbos, difficulty was experienced in equating one community with another. This is due to high geographic turnover (gamma diversity) of species in roughly similar montane habitats (Cowling & Holmes 1992). The relationships of communities shown in this paper are open to modification as greater understanding of the composition and functioning of communities is gained. As the synthesis of fynbos proceeds, the recognition of regional associations of limited extent or geographical races of an association may have to be recognized (Werger *et al.* 1972; Cowling & Holmes 1992) to overcome the problems of equivalence between communities. For instance this may ultimately result in the recognition of southwestern Cape, southern Cape and southeastern Cape zones of the Fynbos Biome.

The vegetation of the BWA was almost completely burned in a summer wildfire in February 1988, subsequent to the sampling of relevés reported on here. After three years (April 1991), apart from the predominance of 'fire-ephemerals' such as *Ursinia trifida* which dominate over large parts of the south slopes, the communities of BWA as described here are identifiable. As succession proceeds it is predicted that the robustness of the floristic classification will become even more evident as the fire ephemerals disappear and the perennial shrublands reach their mature expression.

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The vegetation of the southern Langeberg, Cape Province. 2. The plant communities of the Marloth Nature Reserve

D.J. MCDONALD*

Keywords: classification, forest, fynbos, Langeberg, phytosociology

ABSTRACT

The Marloth Nature Reserve, encompassing the mountain catchments of the southern Langeberg immediately above Swellendam, Cape Province, South Africa, is described. The vegetation of the reserve was sampled along a transect representing the variation in plant communities over the range from the lower south to the lower north slopes. Eighty-three sample sites were subjectively located in mature stands of fynbos vegetation (>10 years old). The relevé data were initially classified using TWINSPLAN and then refined by Braun-Blanquet (BB) phytosociological procedures. The Afromontane Forest patches which occur mainly on the lower south slopes were not sampled but are briefly discussed. The fynbos plant communities are described, based on tables, and a hierarchical classification is proposed.

UITTREKSEL

Die Marloth Natuurreservaat wat die bergopvanggebiede van die suidelike Langeberge bokant Swellendam, Kaaprovinsie, Suid-Afrika, insluit, word beskryf. Die plantegroei van die reservaat is versamel langs 'n transek wat die variasie in plantgemeenskappe oor die bergreeks vanaf die onderste suidelike tot die onderste noordelike hange verteenwoordig. Drie-en-tagtig monsterpersele is subjektief in volwasse fynbos (>10 jaar oud) uitgelê. Die relevé-data is aanvanklik deur middel van TWINSPLAN geklassifiseer en toe deur Braun-Blanquet (BB) fitososiologiese prosedures verfyn. Die Afro-montane woudgemeenskappe wat hoofsaaklik op die onderste suidelike hange voorkom, is nie gemonster nie maar word kortliks bespreek. Die fynbosplantgemeenskappe word kortliks beskryf, gebaseer op tabelle, en 'n hiërgiesse klassifikasie word voorgestel.

CONTENTS

Introduction 153

Study area 154

Location 154

Physiography 154

Geology 156

Soils 156

Climate 157

Methods 157

Vegetation 158

Afromontane Forest 158

Fynbos 158

1. *Cliffortia serpyllifolia* Shrublands of the lower south slopes 158

1.1 *Cliffortia serpyllifolia*–*Widdringtonia nodiflora* Shrublands 158

1.1.1 *Widdringtonia nodiflora*–*Rhodocoma fruticosa* Shrublands (A) 158

1.2 *Cliffortia serpyllifolia*–*Leucadendron eucalyptifolium* Shrublands 159

1.2.1 *Leucadendron eucalyptifolium*–*Hippia pilosa* Shrublands (B) 163

1.2.2 *Leucadendron eucalyptifolium*–*Erica vestita* Shrublands (C) 164

2. *Erica hispidula* Shrublands of the high elevation zone 165

2.1 *Erica hispidula*–*Brunia alopecuroides* Shrublands (D) 165

2.2 *Erica hispidula*–*Berzelia intermedia* Shrublands (E) 166

2.2.1 *Berzelia intermedia*–*Erica conferta* Shrublands (F) 166

2.2.2 *Berzelia intermedia*–*Grubbia rosmarinifolia* Shrublands (G) 167

2.2.3 *Berzelia intermedia*–*Cliffortia grandifolia* Shrublands (H) 168

2.3 *Erica hispidula*–*Pentaschistis malouinensis* Shrublands (I) 168

2.3.1 *Pentaschistis malouinensis*–*Tetraria bromoides* Shrublands (J) 169

2.4 *Erica hispidula*–*Hypodiscus aristatus* Shrublands (K) 169

2.4.1 *Hypodiscus aristatus*–*Phylica pinea* Shrublands (L) 170

2.4.2 *Hypodiscus aristatus*–*Erica versicolor* Shrublands (M) 170

2.4.3 *Hypodiscus aristatus*–*Restio strictus* Shrublands (N) 171

2.4.4 *Hypodiscus aristatus*–*Erica multumbellifera* Shrublands (O) 171

3. *Leucadendron eucalyptifolium* Shrublands of the extreme north slopes 172

3.1 *Leucadendron eucalyptifolium*–*Erica melanthera* Shrublands (P) 172

3.2 *Leucadendron eucalyptifolium*–*Hypodiscus argenteus* Shrublands (Q) 172

Discussion and conclusions 173

Acknowledgements 174

References 174

INTRODUCTION

This paper is the second in a series describing the plant communities of the southern Langeberg, Cape Province. The fynbos plant communities occurring in the Marloth Nature Reserve (Swellendam State Forest) are described and classified. The Afromontane Forest patches found in the study area were not sampled but are briefly discussed based on the studies of McKenzie (1978).

* National Botanical Institute, P.O. Box 471, Stellenbosch 7599.
Present address: Conservation Biology Unit, NBI Kirstenbosch, Private Bag X7, Claremont 7735.
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STUDY AREA

Location

The Marloth Nature Reserve (MNR) is situated in the mountain catchments of the southern Langeberg above the town of Swellendam (Figure 1). In 1928 a deputation of Swellendam residents petitioned the Minister of Lands and Forestry, General Kemp, to set aside a part of the mountain behind Swellendam as a nature reserve. The well-respected chemist and botanist Dr Rudolf Marloth proposed approximately 190 ha on the lower slopes of the Langeberg behind Swellendam, as a suitable area. This area which included the forest patches of Koloniesbos and Duiwelsbos, was proclaimed as a nature reserve and named in honour of Dr Marloth (Lückhoff 1981).

More recently, in accordance with the policy of the former Directorate of Forestry and Environmental Conservation to extend reserves for more effective management, the MNR was enlarged to more than 11 000 ha in June 1981. At the same time the Swellendam Hiking Trail was opened for recreational hiking in the MNR (Lückhoff 1981). Similar to the Boosmansbos Wilderness Area, the MNR is bounded on the north and south sides largely by agricultural lands and on the west and east sides by privately owned mountain land.

The sample transect selected in the MNR extended from the lower south slopes at the foot of 12 O'Clock Peak to the 'Plaaf' or plateau and from there up the south-facing slopes of 12 O'Clock Peak. The transect was then 'broken' and continued from 10 O'Clock Peak down the north-facing slopes into Boskloof Valley and up the opposite south-facing slope to the summit of Hermitage Ridge. From this point samples were taken, roughly following

the route of the Swellendam Hiking Trail to Goedgeloof Hut on the extreme lower north slopes of the range. This route gave ready access to the area. Although the transect covered a narrow belt and consequent relatively small area compared with the whole MNR, it allowed for sampling of the variety of fynbos plant communities present (Figure 2).

Physiography

The south slopes of the Langeberg above Swellendam are steep and rise rapidly to the famous 'Clock Peaks' (Figure 3). On the lower south slopes, however, the steepness is broken by the 'Plaaf' at an elevation of approximately 500 m. This plateau is the result of down-faulting of the Worcester Fault along this part of the Langeberg Range. On the north side of 10 to 12 O'Clock Peaks the slopes drop steeply into the Boskloof intermontane valley (Figure 4). Between 12 O'Clock Peak and One O'Clock Peak to the west is the deeply faulted, dissected and inaccessible Hermitage Kloof. This kloof lies below Hermitage Peak (1 154 m) and Misty Point or Goedgeloof Peak (1 710 m), the highest peak of the Langeberg. To the north of and overlooking Boskloof Valley is the rocky Hermitage Ridge, which gives way in turn to the dissected area of Zuurplaats and the open high-altitude valley of Langkuilen. North of Langkuilen is Goedgeloof Ridge which lies adjacent to the Little Karoo. West of Misty Point is Protea Valley which extends westwards over Dwariganek into the Twistniet Valley. The topography from Protea Valley westwards to Nootgedacht River is dominated by a series of peaks; Kruispad Peak (1 365 m), Leeurivierberg (1 628 m), Middelrivierberg (1 405 m) and Klipspringerkop (1 127 m). The south slopes of these peaks are steep but uniform and not deeply

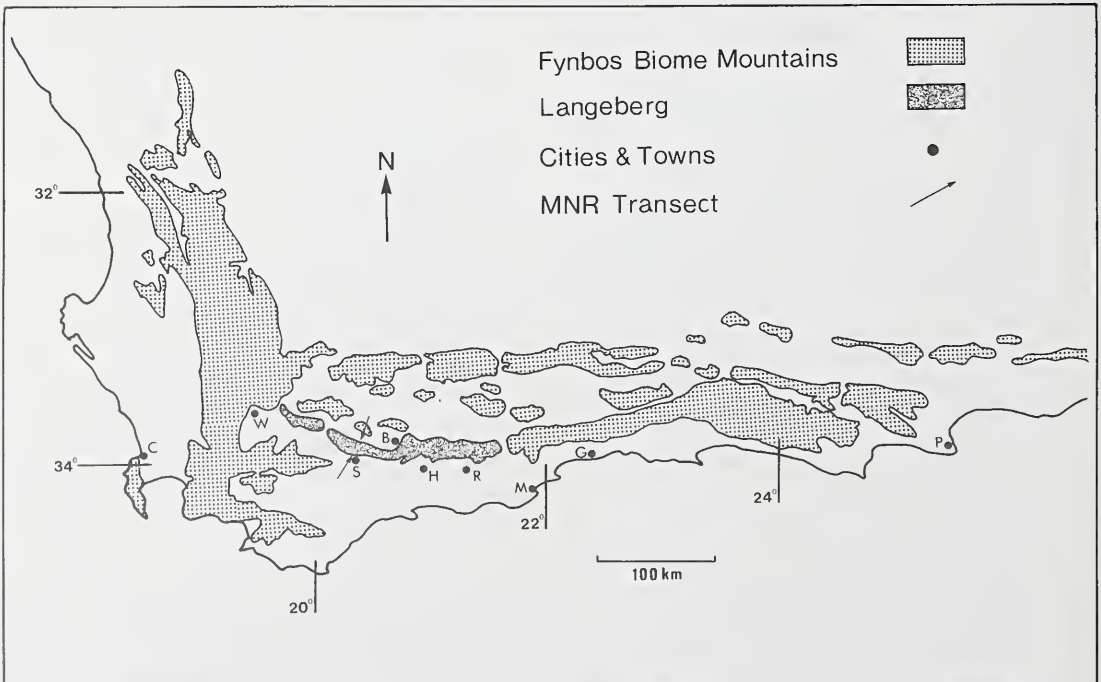


FIGURE 1. — Map of the mountains of the Fynbos Biome showing the position of the Langeberg and the location of the Marloth Nature Reserve (MNR) transect. B, Barrydale; C, Cape Town; G, George; H, Heidelberg; M, Mossel Bay; P, Port Elizabeth; R, Riversdale; S, Swellendam and W, Worcester.



FIGURE 2.—Portion of topographical map 3320CD Scheepersrus, showing part of the MNR with positions of the sample plots. (Map reproduced under Government Printer's copyright authority dated 30 October 1991).



FIGURE 3.—The steep south-facing slopes of the Langeberg above Swellendam. Photograph taken from Twelve O'Clock Peak.

dissected. In contrast, the north slopes are much more dissected and less uniform, particularly when compared with the north slopes below Misty Point.

Leeukloof, Wolfkloof, Hermitage Kloof, and Boskloof drain the mountain catchments of the area to the south and southeast. On the north slopes numerous streams such as the Rietrivier, Knapsakkraalrivier, Warmwaterrivier and Dwarigarivier have their sources at high altitude and drain the dry north-facing slopes, supplying water for agriculture on the north flank of the Langeberg.

Geology

Extending from Goudini, which lies beyond the Langeberg in the northwest, along the lower southwest side of the Langeberg, to the proximity of Sparrebosch (immediately east of Swellendam) is a 'band' of Malmesbury Group sediments. The exposure of these sediments follows the Worcester Fault and in the MNR they are found on the lower slopes of the peaks listed above, but below the 'Plaat' (i.e. below 500 m) (De Bruyn *et al.* 1974).

The main massif of the mountain in the MNR is composed of Table Mountain Group (TMG) sediments. All the high peaks on the south side of the Langeberg Range

in the MNR consist of Peninsula Formation sandstone. Hermitage Peak and Misty Point, which have a more northerly position, consist of Nardouw Subgroup sandstones (South African Committee for Stratigraphy, SACS 1980). The distinction can be made by tracking the position of the intervening Cedarberg Formation shaleband. Soils derived from weathered Cedarberg Formation shale are encountered in the Boskloof Valley westwards to Hermitage Kloof. The extreme folding in Hermitage Kloof obscures the position of the shaleband, but it is once again evident in Protea Valley, at Dwariganek and into the Twistniet Valley.

A silcrete mesa extends from the base of the Langeberg below Goedgeloof Ridge northwards. The Nardouw Subgroup sandstones of the northernmost slopes thus make contact with the silcrete cap which in turn covers the Bokkeveld Group shales. The silcrete mesa forms a watershed with streams draining eastwards to the Tradouws River and westwards to the Kingna River.

Soils

The soil forms (Soil Classification Working Group 1991) occurring in MNR are summarized in Table 1, indicating their parent material, diagnostic characteristics and position in the landscape. No attempt has been made to



FIGURE 4.—Boskloof, behind the Clock Peaks, as seen from the high altitude south-facing slopes of Hermitage Ridge.

TABLE 1.—Soils of the Marloth Nature Reserve

Soil form	Parent material	Diagnostic characteristics	Position in landscape
Champagne	Organic matter	> 200 mm deep, plant remains	Cool, moist, high alt. slope, S-aspect
Houwhoek	Peninsula Formation sandstones	Orthic A-horizon, E-horizon, podzol-B overlying saprolite	S-facing slopes at mid- to high altitudes, with high rainfall
Cartref	Peninsula Formation sandstones	Orthic A-horizon, E-horizon, lithocutanic B-horizon	S-facing slopes at mid- to high altitudes, with high rainfall
Clovelly	Malmesbury Group and Cedarberg Formation shales	Orthic A-horizon with yellow-brown apedal B-horizon	Below the 'Plaat' and on exposure of Cedarberg shale in Boskloof & Protea Valley
Glenrosa	Peninsula Formation & Nardouw Subgroup sandstones	Orthic A-horizon with lithocutanic-B	Rocky, N-facing slopes with lower rainfall
Mispah	Peninsula Formation & Nardouw Subgroup sandstones	Orthic A-horizon over hard rock	Ridge crests, rock outcrops and N-aspect rocky slopes

identify all possible soil forms found in MNR, but rather to give a broad overview of major forms; particularly those encountered on the sample transect.

Climate

Climatic data for Langeberg montane environments are scant and the climate measured at the Swellendam and Weltevrede weather stations (Soil and Irrigation Research Institute, SIRI 1986), i.e. those stations closest to the MNR, does not accurately represent the montane climate. Climate diagrams for these stations, Figure 5A & B, represent the climates at the lower south and north extremes of the MNR transect.

The climate of the MNR is typical of the southern Langeberg since it falls within the transition zone between winter and year-round rainfall areas. The mean annual precipitation for the high peaks is estimated to be more than 1 400 mm (Dent *et al.* 1987). However, the climate on the south side of the range is distinctly different from that on the north side. The south slopes of the southern Langeberg experience the highest rainfall in autumn (April) and late winter to spring (August and October) with rainfall in excess of 40 mm for every month except May, the driest month. This bimodality is not evident in the rainfall pattern on the north slopes of the range which are in a rainshadow. Here a peak in rainfall occurs in autumn (April) with a dry period in May preceding a somewhat elevated winter to spring rainfall, Figure 5A. The rainfall exceeds 40 mm only in April and August. The mean summer maximum and mean winter minimum temperatures for Swellendam are 29.4°C (January) and 6.6°C (July) respectively. On the opposite side of the mountain at Weltevrede (33° 56' S, 20° 37' E), on the lower north slopes of the Langeberg, the equivalent temperatures are 30.0°C (February) and 2.9°C (July), Figure 5B.

The windiest months at Weltevrede are December and February and at Swellendam, May. Hot, strongly desiccating föhn-like berg winds occur mainly in May, June and July.

METHODS

During 1988, 1989 and 1990, 83 plots were sampled along a predetermined transect in the study area (Figure 2). The area was not stratified since no suitable aerial

photographs were available. Consequently plots were subjectively placed in what were taken as the major landscape features and plant communities. The rectangular sample quadrats were 50 m², subdivided into 10 equal-sized subplots to facilitate data collection (McDonald 1988, 1993). Only permanently recognizable species were recorded. Geophytes and annuals encountered were noted but not used in the analyses. The Braun-Blanquet cover-abundance scale (Mueller-Dombois & Ellenberg 1974; Werger 1974) was applied. A border zone of 1.5 m from the perimeter of each plot was rapidly searched for any additional species not found in the marked plot.

Only the sclerophyllous fynbos was sampled since the mixed evergreen (Afro-montane) forests are well documented by McKenzie (1978).

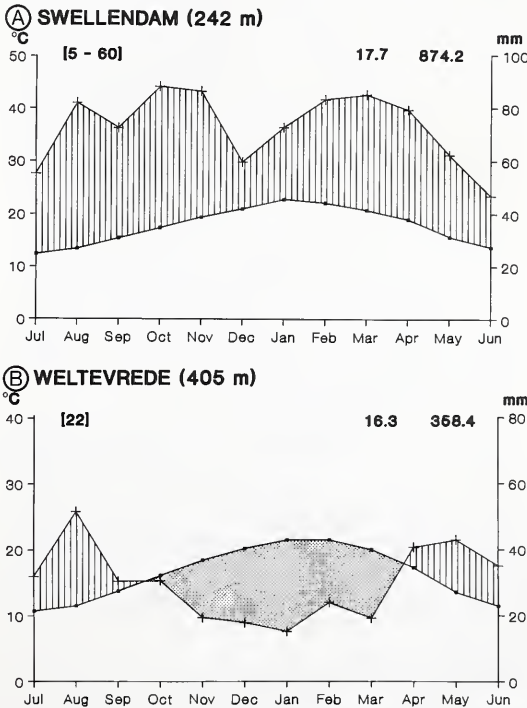


FIGURE 5.—Walter-Lieth climate diagrams for A, Swellendam and B, Weltevrede, on the northern side of the Langeberg.

Phytosociological tables were compiled by obtaining a 'first approximation' classification using TWINSpan (Hill 1979) and then by successive refinement using Braun-Blanquet procedures with PCTables (Boucher unpublished).

Each community is described following the order in the proposed classification; the structural description follows the system advanced by Campbell *et al.* (1981). Relationships between the communities described here and communities described in other studies of mountain fynbos are given as far as possible. These relationships were determined by comparing the floristic composition of the communities of this study with the respective communities of other studies as indicated below [note that Campbell (1985) gave 'floristics' for each of his lowest level structural units].

VEGETATION

The greater part of the Marloth Nature Reserve is covered by sclerophyllous fynbos typical of the mountains of the western and southern Cape (Taylor 1978; Kruger 1979). Afromontane Forest communities in the MNR are confined to moist kloofs on the south side of the Langeberg range.

Afromontane Forest

Numerous mixed evergreen Afromontane forests (Geldenhuys 1989) are found in the MNR. These forests were exploited for hardwood timber in early colonial days, for wagon-making, furniture and general construction. The accessible forest patches are known variously as Koloniesbos, Duiwelsbos, Doktersbos and Grootbos with less accessible forests being found in Boskloof, Hermitage Kloof, Wolfkloof and Leeukloof. McKenzie (1978) described the '*Rapanea melanophloeos*–*Hartogiella schinoides*–*Podocarpus latifolius* Forest Association' as the general type found in the southwestern Cape. This association was divided into three subassociations, two of which are found in the MNR: *Cunonia capensis*–*Platylophus trifolius* Subassociation and *Carissa bispinosa*–*Canthium ventosum*–*Canthium mundianum*–*Pterocelastrus tricuspidatus* Subassociation. Only one of the variations of the *Cunonia capensis*–*P. trifolius* Subassociation, the *Cunonia capensis*–*Todea barbara* Variation was identified in MNR, whereas two variations of the second subassociation, *Buddleja saligna*–*Scolopia mundii* Variation and *Rothmannia capensis*–*Olinia ventosa*–*Canthium ventosum*–*Canthium mundianum* Variation were identified (McKenzie 1978).

The three variations of forest subassociations identified in MNR occur on a moisture gradient. The *Cunonia capensis*–*Todea barbara* Variation occurs in wet situations along streams, the *Rothmannia capensis*–*Olinia ventosa*–*Canthium ventosum*–*Canthium mundianum* Variation is found on seasonally wet to dry sites and the *Buddleja saligna*–*Scolopia mundii* Variation on relatively dry sites.

Fynbos

The complexity of the fynbos vegetation of the Marloth Nature Reserve has necessitated subdivision of the data

into three parts for treatment in separate phytosociological tables (Tables 2, 3 & 4). These subdivisions represent logical separations which have facilitated definition of the fynbos shrubland communities.

The TWINSpan analysis separated the data into 23 subdivisions. The division at Level 1 indicated the separation of the data into two groups; relevés in Tables 2 & 3 on the one hand and Table 4 on the other. TWINSpan separated the relevés of Table 4 into two groups at Level 2 and finally into three subdivisions at Level 3; a finer classification than presented in Table 4.

At Level 2, the remaining relevés are separated into two groups; communities A–C and I–O on the one hand and communities D–H on the other. At Level 3 communities A–C (Table 2) are separated from communities I–O which are treated together with communities D–H in Table 3. At the lower levels of the TWINSpan classification there is some agreement between this analysis and the BB-classification, however, the latter classification is favoured since it yields fewer units that are more easily interpreted and identified in the field.

1. *Cliffortia serpyllifolia* Shrublands of the lower south slopes

The shrublands of the lower south slopes of the Langeberg at Swellendam are conspicuously dominated by *Cliffortia serpyllifolia* which is hardly found higher than the edge of the 'Plaat'. The edge of the 'Plaat' represents the contact between the TMG sediments and the basement rock of the Malmesbury Group with which *C. serpyllifolia* appears to be strongly associated. A logical separation of the lower slope plant communities on Malmesbury Group sediments [Main Quartzite of the Lower Group of the Boland Formation (De Bruyn *et al.* 1974)] (Table 2) from the *Erica hispidula* shrublands (Table 3) of higher elevation on TMG sediments is therefore possible. It is important to note, however, that many of the species are common to both shrubland types.

1.1 *Cliffortia serpyllifolia*–*Widdringtonia nodiflora* Shrublands

Only one poorly defined shrubland community is included here. This community lies at the transition between the *Erica hispidula* Shrublands of the high elevation zone and the *Cliffortia serpyllifolia*–*Leucadendron eucalyptifolium* Shrublands.

1.1.1 *Widdringtonia nodiflora*–*Rhodocoma fruticosa* Shrublands (A)

Differential species: *Rhodocoma fruticosa*, *Tetraria brevicaulis*, *Ehrharta ramosa*, *Tetraria ustulata*, *Edmondia sesamoides*, *Ursinia nudicaulis*.

Dominant species: *Cliffortia serpyllifolia*, *Erica hispidula*, *Erica versicolor*, *Penaea cneorum subsp. ruscifolia*.

Structural formation: Mid-high, Mid-dense (Ericoid) Shrubland with a Mid-dense Graminoid Shrubland Understorey.

Relationships: unclear.

TABLE 3.—A phytosociological table of the *Erica hispidula* Shrublands along a transect through the Marloth Nature Reserve, Langeberg, Swellendam (continued)

Relevé Number *1222*11112*11111111*1111112*11111*1111*11111*11112*11111111*111112*111*11
 *7000*55550*33344566*3566660*44569*6777*77789*79990*44444788*688990*678*99
 *9456*56787*67957401*8323452*08996*7456*13780*83781*12346209*627123*801*45

Species common to Communities E, F, G & H									
Tetraria compressa Turrill	RR+	.1	11.0+	111	.0	+	.	.	.
Calopsis membranacea (Pillans) Linder	0+2	.	.	211
Ursinia serrata (L.f.) Poir.	++	.	+	0
Osmitopsis osmitoides (Less.) Bremer	+++1	.	1	.01	++1+	.R	1	.	.
Gnidia galpinii C.H. Wr.	++	.++	.	R
Thesium carinatum A. DC.	+	.	0	.	.	+	.	.	.
Indigofera concava Harv.	++R.	.	.	+	R	.	+	+	.
Differential species of the Pentaschistis malouinensis--Tetraria bromoides Shrublands (J)									
Tetraria bromoides (Lam.) Pfeiffer	2++3	.	.	.
Protea aurea (Burm. f.) Rourke subsp. aurea	31	.	.	.
Erica pubigera Salisb.	1	.	.	.
Leucadendron salignum Berg.	1	.	.	.
Leucadendron eucalyptifolium Buek ex Meisn.	+	0	3	1	.
Helichrysum pandurifolium Schrank	R	.	.	.	+	.	++11	.	.
Species common to communities E, F, G, H & J									
Helichrysum felinum (Thunb.) Less.	0	+	.	R.	1	++.	.	+	+
Erica cubica L.	.	.	.1210	3	.	.	1	4.02	+
Elegia capensis (Burm. f.) Schelpe	++11	.	1	2	.10	+	.	1	.
Hypodiscus albo-aristatus (Nees) Mast.	2	.	.	1.	121	.2	.	.5	3
Erica cordata Andr.	++	1	2	4
Pteridium aquilinum (L.) Kuhn	+	.	.	00	+
Differential species of the Erica hispidula--Pentaschistis malouinensis Shrublands (I)									
Pentaschistis malouinensis (Steud.) Clayton	021	.	.212	.
Differential species of the Hypodiscus aristatus--Phylica pinea Shrublands (L)									
Phylica pinea Thunb.	+	.	.	.	00121
Tetraria thermalis (L.) C.B. Cl.	11
Ceratocaryum decipiens (N.E. Br.) Linder	23
Erica atropurpurea Dulfer0	.	.	++
Species common to communities E, F, G, H, I, J & L									
Widdringtonia nodiflora (L.) Powrie	0+12	.+0+	11+	.+010	+12.0	1	.0112	.11	.+ 200
Blechnum tabulare (Thunb.) Kuhn	+1	R2+2	.1	0	01	.00R210	.1	+	. 1 . 1 .
Bobartia macrospatha Bak. subsp. macrospatha	0	+01	+	.000	.+ +
Epischoenus dregeanus (Boeck.) Levyns	+1	.	.	+	1	.1	1	. 1 .111	1.
Ursinia scariosa (Ait.) Poir. subsp. subhirsuta	.	.	.	0	+	+	.	.	++
Ehrharta ramosa (Thunb.) Thunb.	.	.	.	+	.	.	.	+	+
Cassytha ciliolata Nees	.	+	.	.	+	.	.	.	+
Species common to communities I, L & M									
Erica versicolor Wendl.	1.	.	.	+	31115.20+ ++3

TABLE 3.—A phytosociological table of the *Erica hispidula* Shrublands along a transect through the Marloth Nature Reserve, Langeberg, Swellendam (continued)

Relevé Number *1222*11112*1111111*1111112*11111*1111*1111*11112*1111111*111112*111*11
 *7000*55550*33344566*3566660*44569*6777*77789*79990*44444788*688990*678*99
 *9456*56787*67957401*8323452*08996*7456*13780*83781*12346209*627123*801*45

Differential species of the <i>Hypodiscus aristatus</i> -- <i>Restio strictus</i> Shrublands (N)	
<i>Restio strictus</i> N.E. 8r. 131112 .
Species common to communities O--N	
<i>Erica hispidula</i> L.	++11.435+3.3112 122.4355451.4R54 .042 .325 .12+ +.1 2211++ .2+3210.514
<i>Elegia juncea</i> L.	1222.12212. +.1111+11.1 10 . 12 .11+ .12111.0111+211.1 2111+.1
<i>Anthochortus crinalis</i> (Mast.) Linder	5555. 2113. 1 31 . 1 . 3 32. . 21. . . + 1+ .12
<i>Ehrharta setacea</i> Nees ex Trin. subsp. <i>scabra</i> (Stapf)	11+.+++ +. 1+ . . +. + 1. . .1 2+1+ 1.1121+221.223224.1+2
<i>Chrysithrix capensis</i> L.	2 1.011 2. + 111+ . ++ . . 1 21. 2 +. 2132. +.0+21 . 2232. 21
<i>Platycaulos compressus</i> (Rottb.) Linder	22 . . 1.252222 . 2 1 1 . 21 5. 3 .422 1.+ 1 .1 . + . 1++ . 1
<i>Clutia alaternoides</i> L.	0. . . + . . +. .+++1.1+ 1. + R. ++++ +.1++1+. +
<i>Protea cynaroides</i> (L.) L.	0+1. 0 10.11 10.01 1 0 . 10 . . . + . 10 . 000. 1
<i>Pentaschistis colorata</i> (Steud.) Stapf	+ . 1 2. + 1.12 . +21 .+1121+1 .312222. 2
<i>Senecio cordifolius</i> L.f.	0+1+. ++++ R . +. + ++++ . + + . + . 1 . . R .R + +.
<i>Blaeria coccinea</i> Klotzsch	++21. 1 13.+++ + + . + . . . 2 12. . 1+ + . ++34.
<i>Petalacte canescens</i> DC.	R+ . 1 1. 0 + 1 .3 ++1+.
<i>Kniphofia uvaria</i> (L.) Oken.	0+ +. +. . . . + . + .+++ . . + . . ++
<i>Mairea hirsuta</i> DC.	+ . 21 . . . 1 1+ . + 10 . . 1 . . . ++
<i>Restio fragilis</i> Esterhuysen	1 +. 1. + +
<i>Leucadendron spissifolium</i> (Salisb. ex Knight)	1+ . 0+ . . . 2 . + .2 . . . 2 . + .1
<i>Platycaulos anceps</i> (Mast.) Linder	2 1. 1. . 21. . . 4 . . 4 . + . .
<i>Ensischoenus quadrangularis</i> (Boeck.) C.B. Cl.	1121. 1 .+1111++ + + . 1 . +.
Species common to communities E--N	
<i>Lobelia neglecta</i> Roem. & Schult.	++ . . . + ++++ . +. +. +. + . + +R. + + +. . +
<i>Edmondia sesamoides</i> (L.) Hilliard	++ . 0 . . . + .0+ +.0 0 . + .122+2 12.22+0 . + +
<i>Tetraria brevicaulis</i> C.B. Cl.	++1 R. + . + . R. . 1 .111 1.1++ 1.1+1+1+1+ . +++ 1 1
<i>Penaea cneorum</i> Meerb. subsp. <i>ruscifolia</i> Dahlg.	223 .++1+ 1 +.++22222.2 2 + 1 .4 + . + 2.0 +211++ . 1 . ++
<i>Centella lanata</i> Compton	+ 1 2.1++ ++. 2++1+ . + + 0 . + +. ++
<i>Psoralea pinnata</i> L.	+ + . 0 . . + ++1+ .1 10 . . . +1++ . R 2 . . 1
<i>Erica daphniflora</i> Salisb.	+++ . + . . . + .3411. +1 . . 1+ . 2131 .
<i>Tetraria flexuosa</i> (Thunb.) C.B. Cl.	1112 . 1.212+3. + 1 . . + .1 1. 2
<i>Struthiola eckloniana</i> Meisn.	. + 1. ++ +1+ . . . + .+1 +. . + .
<i>Corymbium glabrum</i> L. var. <i>glabrum</i>	++ +. R0+1+1 ++.11++++.1 1
<i>Metalasia densa</i> (Lam.) Karis	. R . . . R. +. . + .112++ 2+.11++ . 1
<i>Chondropetalum mucronatum</i> (Nees) Pillans	.+21+ 4. 02. . 1 .2 + R .
<i>Gleichenia polypodioides</i> (L.) J.E. Sm.	++ 4 . .+1 + + . 10+. .
<i>Indigofera sarmentosa</i> L.	R+ . . +R +. + . . . + +. . + .
<i>Schizaea pectinata</i> (L.) Sw.	+ . . + R. 1+++ . + . +
<i>Anemone tenuifolia</i> (L.f.) DC.	OR . . + +. . + +1
<i>Bobartia parva</i> J.B. Gillett	. +1 ++ . + . R .
<i>Euryops pinnatifidus</i> (DC.) B. Nord.	+ . . . 1. . + . + . +. . + .
<i>Tetraria capillacea</i> (Thunb.) C.B. Cl.	+ 1 22 . . 1
<i>Ursinia scariosa</i> (Ait.) Poir. subsp. <i>scariosa</i>	R++ . . . + +
<i>Erica bracteolaris</i> Lam.	. . . + . + . . 1 . . 1 . . 1
<i>Othonna quinqueidentata</i> Thunb.	1 +0.R +
<i>Osteospermum corymbosum</i> L.	+ 0+ . . + . .
<i>Centella stenophylla</i> Adanson	. . . 2. 1 2+ . . .
<i>Restio triticeus</i> Rottb.	11 . + + . . .

TABLE 3.—A phytosociological table of the *Erica hispidula* Shrublands along a transect through the Marloth Nature Reserve, Langeberg, Swellendam (continued)

Releve Number

*1222*11112*11111111*111112*11111*1111*11112*11111111*111112*111*11
*7000*55550*33344566*3566660*44569*6777*77789*79990*44444788*688990*678*99
*9456*56787*67957401*8323452*08996*7456*13780*83781*12346209*627123*801*45

Species common to Communities E--N

Restio decipiens (N.E. 8r.) Linder	1.	.	3	2	.
Senecio ilicifolius (L.) Thunb.	.	.	.	R.	.	+	+
Ursinia nudicaulis (Thunb.) N.E. 8r.	.	0	.	.	.	1	+++	+	OR+++	+	+
Cliffortia heterophylla Weim.	.	.	0	2+	+	.	.25
Stoebe spiralis Less.	+	1	1+	++
Stoebe plumosa (L.) Thunb.	.	0111+	.	.	1	+	0
Centella montana Adamson	++ R	+	+
Tetraria crassa Levyns1	.	.	.1	+	.1
Restio capillaris Kunth1	.	.	1	.	.
Erica ardens Andr.	.	.	.	+.R	.	.	+	.	1+	+	+
Erica imbricata L.	.	.	.	4.	.	.0	+.0	+.2	+	.0+	+

Differential species of the Hypodiscus aristatus--Erica multumbellifera Shrublands (0)

Staberoha cernua (L.f.) Dur. & Schinz	41
Erica multumbellifera Berg.	+2

Species common to communities K, L, M, N & O

Thamnochortus cinereus Linder0	+	1	1+	1++	+++01.2+	++
Hypodiscus aristatus (Thunb.) Krauss	21	.1222122.	11	+.2+	20
Cliffortia densa Weim.	.	.	.	R.	2+	1.+.110	.	1	1.++
Erica vestita Thunb.	2	2.	1+2	1.	+.R
Pentameris macrocalycina (Steud.) Schweickerdt	.	1.	21	1	1.	2
Stoebe cinerea (L.) Thunb.	+	.	1.	.	.0+

Species common to communities E--O

Tetraria ustulata (L.) C.B. Cl.	221+	.1	32	1.	2211	.331	.	.	.20	.222++	.1+	12	+	.132	+.+	22
Restio inconspicuus Esterhuysen	1	1.	1	.	+	0	.1	1	.2	.21011.	1+1	.11111+	+	.11121.	.112.	1
Tetraria cuspidata (Rottb.) C.B. Cl.	1	+	.	.	+	1	.	3	+.11	.1++	+.1212121.	22	11+	+.12.	++	
Erica melanthera L.	2	.02	4.1	0	+.R	.	.	.	1	++.2+	+	+	0	.41	.	1.35
Drosera aliciae Hamet	R	+	+	R.	RRR	.	+	R	++	R+	.	.	.	++R.	+	++
Ursinia trifida (Thunb.) N.E. 8r.	RR	.	.	+	+	+	+++	+++++	R	+.R	.	
Merkxmuellera lupulina (Thunb.) Conert	.	11	+1	+	2.1+	+	2	+	.	2	21.	1.1++
Calopsis monostylis (Pillans) Linder	.	2R	22.	.1	+	1.	+	+	2.	+	
Ficinia filiformis (Lam.) Schrad.	.	+	+	+	+	+	.1	R	+	1.	.	+
Elegia asperiflora (Nees) Kunth	.	+	1	+
Tetraria compar (L.) Lestib.	.	+	.	.	.1	+	+	

plex geological zone of metamorphism, at the contact between rock of the Malmesbury Group and the Table Mountain Group (see De Bruyn *et al.* 1974). These shrublands reflect the presence of soils derived from shales and other more nutrient-rich sediments.

1.2.1 *Leucadendron eucalyptifolium*—*Hippia pilosa* Shrublands (B)

Differential species: see Table 2.
Dominant species: *Cliffortia serpyllifolia*, *Erica hispidula*, *Erica versicolor*, *Penaea cneorum* subsp. *ruscifolia*,

Tetraria flexuosa.
Structural formation: varies from a Low Closed Graminoid Shrubland with Mid-high Emergent Shrubs to a Mid-high to Tall Closed Shrubland with an Open to Mid-dense Graminoid Understorey.
Relationships: Enon Mesotrophic Proteoid Fynbos (Campbell 1985).

This community (Figure 6) is found at a mean altitude of 447 m (310–570 m) on the cool lower slopes below the 'Plaat'. The parent rock is Peninsula Formation sandstone and all the soils are classified as

TABLE 4.—A phytosociological table of plant communities on the extreme north slopes of the Langeberg, on a transect through the Marloth Nature Reserve, Swellendam

Community		4		Hypodiscus aristatus (Thunb.) Krauss	23 + 0 2 0
		4.2 4.1		Anthospermum galioides Reichenb. f. subsp. reflex.	0 1 11+ +
		P Q		Hypodiscus striatus (Kunth) Mast.	102 2 1+
				Anomalanthus sp. McDonald 1012	22 12 2
Relevé number		*1112*11111		Pentaschistis colorata (Steud.) Stapf	1 111 1
		*4550*88889		Tetraria cuspidata (Rottb.) C.B. Cl.	+ 1+ +1
		*9010*34569		Tetraria thermalis (L.) C.B. Cl.	21 0 0
Altitude (m)		.11 .		Tetraria flexuosa (Thunb.) C.B. Cl.	12 3 1
		.0098.98768		Merxmuellera lupulina (Thunb.) Conert	++ + 1
		.6600.00384		Ceratocaryum decipiens (N.E. Br.) Linder	0 + 1
		.0000.00500		Mastersiella purpurea (Pillans) Linder	1 +
Aspect (°)		.2323.21253		Ischyrolepis capensis (L.) Linder	+ 1
		.5002.50053		Pelargonium fruticosum (Cav.) Willd.	+ +
				Schizaea pectinata (L.) Sw.	+ +

Differential species of the *L. eucalyptifolium*—*Erica melanthera* Shrublands (P)

Staberoha cernua (L.f.) Dur. & Schinz	11 2
Ursinia nudicaulis (Thunb.) N.E. Br.	++ R
Erica melanthera L.	24 0
Penaea cneorum Meerb. subsp. ruscifolia Dahlg.	11 +
Psoralea pinnata L.	+R+
Erica spectabilis Klotzsch	RR
Struthiola eckloniana Meisn.	++
Restio inconspicuus Esterhuysen	1
Lightfootia tenella Lodd.	0
Chrysithrix capensis L.	+
Phyllica mairei Pillans	+
Elegia juncea L.	1
Tetraria involucrata C.B. Cl.	0
Tetraria capillacea (Thunb.) C.B. Cl.	1
Phyllica pinea Thunb.	1
Thamnochortus cinereus Linder	+
Gleichenia polypodioides (L.) J.E. Sm.	+
Festuca scabra Vahl	1
Aspalathus verbasciformis Dahlg.	+
Lobelia neglecta Roem. & Schult.	0
Erica hispidula L.	+
Ficinia cf. paradoxa (Schrud.) Nees	+
Tetraria brevicaulis C.B. Cl.	+
Cliffortia pterocarpa (Harv.) Weim.	1
Erica vestita Thunb.	1
Restio scaberulus N.E. Br.	+
Bobartia parva J.B. Gillett	+
Pentaschistis acinosa Stapf	1
Edmondia sesamoides (L.) Hilliard	0

Differential species of the *Leucadendron eucalyptifolium*—*Hypodiscus argenteus* Shrublands (Q)

Hypodiscus argenteus (Thunb.) Mast.	1+101
Lobelia capillifolia (Presl.) A. DC.	+++++
Lanaria lanata (L.) Dur. & Schinz	2112
Heteropogon contortus (L.) Roem. & Schult.	++1
Ehrharta ramosa (Thunb.) Thunb.	0 + 0
Agathosma ovata (Thunb.) Pillans	22 1
Ficinia nigrescens (Schrud.) Raynal	++ +
Willdenowia glomerata (Thunb.) Linder	1++
Stoebe aethiopica L.	0 + +
Tetraria sp. McDonald 1848	++
Ursinia scariosa (Ait.) Poir. subsp. scariosa	+0
Ficinia monticola Kunth	++
Maytenus oleoides (Lam.) Loes.	0+
Corymbium glabrum L. var. glabrum	+ 1
Leucospermum calligerum (Salisb. ex Knight) Rourke	22
Syncarpha paniculata (L.) B. Nord.	++
Selago sp. 183/20	++
Prismatocarpus brevifolius A. DC.	++
Centella glabrata L. var. glabrata	+
Crassula atropurpurea (Haw.) Dietr. var. atropurp.	+
Felicia filifolia (Vent.) Burt Davy subsp. bodkin.	+
Anthospermum spathulatum Sprengel subsp. spathulatum.	1
Lobelia coronopifolia L.	+
Rhodocoma fruticosa (Thunb.) Linder	+
Thoracosperma galpinii N.E. Br.	2
Tetraria crassa Levyns	+
Erica plukenetii L.	+
Widdringtonia nodiflora (L.) Powrie	0
Restio strictus N.E. Br.	+
Askidiosperma paniculatum (Mast.) Linder	1

Species common to Communities P & Q

Leucadendron eucalyptifolium Buek ex Meisn.	2334 33++3
Tetraria ustulata (L.) C.B. Cl.	2213 22221
Stoebe spiralis Less.	+0++ ++ +
Elegia galpinii N.E. Br.	1 30 211 2
Restio filiformis Poir.	1+ 21121
Elegia fistulosa Kunth	1 1++11
Restio triticeus Rottb.	1+1 2 1+

Glenrosa Form. Aspect of the sample sites is mainly southerly, ranging from east-south-east to south-south-west. Mean gradient is 23.4° (14°–32°, n = 5). Rock cover is low (<1%) with one exception of 25% in plot 133. Litter cover is conversely high ranging from 70–85%, with vegetation cover 100% in all samples.

This community is weakly differentiated but has strong affinity to the *Penaea cneorum*–*Widdringtonia nodiflora* Shrublands described below. The most striking feature is the dominance of *Cliffortia serpyllifolia*.

1.2.2 *Leucadendron eucalyptifolium*–*Erica vestita* Shrublands (C)

Differential species: *Erica vestita*, *Lanaria lanata*, *Cymbopogon marginatus* and others, see Table 2.

Dominant species: *Cliffortia serpyllifolia*, *Erica hispidula*, *Leucadendron eucalyptifolium*, *Penaea cneorum* subsp. *ruscifolia*.

Structural formation: Mid-high to Tall Sparse to Closed Proteoid Shrubland with a Low Closed Graminoid Shrubland Understorey or a Low Closed Ericoid Shrubland with a Mid-dense Graminoid Understorey.

Relationships: Enon Mesotrophic Proteoid Fynbos (Campbell 1985).

This community (Figure 7) is found on the complex zone of Malmesbury Group sediments which are exposed below the 'Plaai'. There is strong correlation between this community and the relatively nutrient rich soils of the Malmesbury Group sediments. The soils of relevés 127, 128 & 130 were 0.2–0.3 m deep and classified as Glenrosa Form, whereas those of relevés 125 and 126 exceed 1.0 m and were classified as Clovelly Form soils. The five relevés were sampled at a mean elevation of 283 m (242–320 m) with a mean gradient of 12.2° (5°–20°). Cover of exposed rock was recorded as nil except for sample plot 127 where a high value of 90% was recorded. Vegetation cover averaged 96% and litter cover 66%. Four of the five sample sites had a westerly aspect with the remaining one on a northeast-facing slope.

Erica vestita is a prominent, easily identifiable differential species in this community. It has three colour forms, two of which are found on the Langeberg. The colour form found in the *Leucadendron eucalyptifolium*–*Erica vestita* Shrublands below the 'Plaai' is pink, whereas in the *Erica hispidula*–*Hypodiscus aristatus* Shrublands (described below) the flowers are crimson red. Of further particular note in this community are *Lanaria lanata*, *Cymbopogon marginatus* and *Erica pubigera* which appear to favour



FIGURE 6.—The *Widdringtonia nodiflora*–*Hippia pilosa* Shrublands on the lower south slopes of MNR below the 'Plaat', with tall *Leucadendron eucalyptifolium* in the foreground.

2. *Erica hispidula* Shrublands of the high elevation zone

The *Erica hispidula* Shrublands described in this paper are broadly equivalent to those described by McDonald (1993). *E. hispidula* is present in all but one community, the *Hypodiscus aristatus*–*Erica multumbellifera* Shrublands. Speculation as to the reason for this absence is given below in the description of the latter community. *Restio inconspicuus*, which assumes a distinctive yet subordinate position to *E. hispidula* in the shrublands of Boosmansbos Wilderness Area (McDonald 1993), is less prominent in MNR.

2.1 *Erica hispidula*–*Brunia alopecuroides* Shrublands (D)

Differential species: *Brunia alopecuroides*, *Carpacoe spermacoea*, *Erica curviflora*, *Erica ominoglabra*, *Hippia integrifolia*, *Mairea microcephala*, *Stylapteris dubius*.

Dominant species: *Anthochortus crinalis*, *Brunia alopecuroides*.

Structural formation: Low to Mid-high Closed Brunioid Shrubland with Closed Restioid Understorey.

Relationships: *Brunia alopecuroides*–*Restio bifidus* Community (Kruger 1974); *Simocheilus carneus*–*Restio*

anceps Community (Bond 1981), Ruittersberg Wet Erica-ceous Fynbos (Campbell 1985).

Similar to the *Erica hispidula*–*Spatalla nubicola* Shrublands of BWA (McDonald 1993), the *Erica hispidula*–*Brunia alopecuroides* Shrublands are found mainly on the high altitude south- to southwest-facing slopes of the peaks and ridges of the MNR, in the cool, moist 'mist zone' (Figure 8). The substratum consists of decomposed organic material, forming a deep acid peat, which is classified as Champagne Form soil.

Although the Community is found on the Clock Peaks, it was not sampled here. Most sample plots (204, 205 & 206) were located on the high-altitude south-facing slopes of Hermitage Ridge, overlooking Boskloof, with one sample (Relevé 179) situated above the south tributary of Zuurplaats Stream.

The *Erica hispidula*–*Brunia alopecuroides* Shrublands typically have a low to mid-high (1.0–1.5 m) closed brunioid-ericoid overstorey, dominated by *Erica curviflora* and *Brunia alopecuroides*. The understorey is dominated by *Anthochortus crinalis* with other herbaceous species playing an inconspicuous role.



FIGURE 7.—The *Leucadendron eucalyptifolium*–*Erica vestita* Shrublands found on the complex zone of Malmesbury Group sediments below the 'Plaat'.



FIGURE 8.—The *Erica hispidula*–*Brunia alopecuroides* Shrublands found on the high altitude south slopes in the 'mist zone'.

Of particular note in this community is the presence of *Erica omninoglabra* (single occurrence in relevé 179), a rare Langeberg endemic species found sprawling amongst the matted restioid understorey, *Klattia partita* (Iridaceae), a shrubby species with non-fugaceous flowers and the endemic *Stylapterus dubius* (Penaeaceae).

2.2 *Erica hispidula*–*Berzelia intermedia* Shrublands

These shrublands include four communities which range from the typical form of the *Erica hispidula*–*Berzelia intermedia* Shrublands (E) to the *Berzelia intermedia*–*Erica conferta* Shrublands on organically rich soils.

Erica hispidula–*Berzelia intermedia* Shrublands 'Typicum' (E)

Differential species: none.

Dominant species: *Erica hispidula*, *Tetraria ustulata*.

Structural formation: Low Closed Ericoid Shrubland with sparse Mid-high Emergent Shrubs.

Relationships: Keurbos Wet Ericaceous Fynbos (Campbell 1985).

The *Erica hispidula*–*Berzelia intermedia* Shrublands (Figure 9) have no differential species but have many species in common with communities F, G and H. These shrublands may therefore be considered as the 'background' of the mosaic of communities found mainly, but not exclusively, on the south- to southeast-facing slopes of Hermitage Ridge and below the Clock Peaks. The relevés (140, 148, 159, 169) representing this community were located at elevations ranging from 600–1 200 m, with a moderate mean gradient of 22.5°. The soils are derived from Peninsula and Goudini Formation sandstone and are classified as Cartref Form. They are well drained and shallow with a mean depth of 0.15 m (0.1–0.2 m) and with a generally low average surface rock cover of 5% (2–10%). Projected vegetation canopy cover, in contrast, is high, ranging from 95–100%.

The dominant stratum of the *Erica hispidula*–*Berzelia intermedia* Shrublands is a Closed Graminoid Shrubland (≤ 1.0 m) with dominance shared by the woody shrubs, *Erica hispidula* and *Penaea cneorum* subsp. *ruscifolia*, the sedges *Tetraria ustulata* and *Tetraria flexuosa* and the ubiquitous *Restio inconspicuus*.

2.2.1. *Berzelia intermedia*–*Erica conferta* Shrublands (F)

Differential species: *Helichrysum capense*.

Dominant species: *Anthochortus crinalis*, *Erica hispidula*, *Elegia juncea*.

Structural formation: Low Closed Ericoid Shrubland either with Sparse Mid-high Emergent Shrubs or a Tall Closed Brunioide Shrubland Overstorey.

Relationships: Ruitersberg Wet Ericaceous Fynbos (Campbell 1985); *Simocheilus carneus*–*Restio anceps* Community (Bond 1981); *Erica hispidula*–*Spatalla nubicola* Shrublands (McDonald 1993).

This community (Figure 10) is represented by five relevés (155, 156, 157, 158, 207). The only true differential species is *Helichrysum capense* since other species characterizing this community, namely *Erica conferta*, *Lobelia pubescens* and *Syncarpha eximia* are shared with



FIGURE 9.—The *Erica hispidula*–*Berzelia intermedia* Shrublands occurring mainly on the south-facing slopes of the Clock Peaks and Hermitage Ridge, forming a 'background' to the mosaic of communities.



FIGURE 10.—The *Berzelia intermedia*–*Erica conferta* Shrublands occurring on moist south-facing slopes below the Clock Peaks and on Hermitage Ridge.

the closely allied *Erica hispidula*–*Brunia alopecuroides* Shrublands. On the sample transect the community is found on the south- and southeast-facing slopes of 12 O’Clock Peak at elevations around 1 000 m, on shallow ‘organic phase’ Cartref Form soils. It is also found on the upper south-southwest-facing slopes of Hermitage Ridge, above Boskloof (relevé 207), where it forms part of a mosaic with the *Erica hispidula*–*Brunia alopecuroides* Community.

The dominant stratum of this community is a low closed ericoid layer dominated by *Erica hispidula* but with a number of other *Erica* species such as *E. cordata*, *E. conferta* and *E. daphniflora*. *Anthochortus crinalis*, *Elegia juncea* and *Tetraria ustulata* are the most important graminoid elements. Emergent from the low stratum in some stands is the fern *Blechnum tabulare*, with a mid-high to tall shrub stratum dominated by *Berzelia intermedia*.

2.2.2 *Berzelia intermedia*–*Grubbia rosmarinifolia* Shrublands (G)

Differential species: *Erica regerminans*, *Grubbia rosmarinifolia*, *Spatalla parilis*, *Raspalia virgata*.

Dominant species: *Erica hispidula*, *Grubbia rosmarinifolia*, *Platyaucos compressus*.

Structural formation: Mid-high to Tall Closed Shrubland with Closed Graminoid Shrubland Understorey.

Relationships: *Brunia alopecuroides*–*Restio bifidus* Community (Kruger 1974); *Chondropetalum*–*Berzelia* Upper Hygic Fynbos (Boucher 1978); Keurbos Wet Ericaceous Fynbos (Campbell 1985).

On the sample transect this community (Figure 11) is found as localized stands on the south-facing midslopes below the Clock Peaks. One sample (Relevé 147) was located at 1 320 m on the south-facing slopes of Goedgeloof Ridge, immediately west of Het Goedgeloofnek. On the mid-slopes of 12 O’Clock Peak at elevations from 600–800 m the community forms part of a mosaic with other communities in the broader *Erica hispidula*–*Berzelia intermedia* Shrublands.

The *Berzelia intermedia*–*Grubbia rosmarinifolia* Shrublands are mainly associated with local, apparently seasonally waterlogged sites. All the relevés typical of this community (136, 137, 139, 147, 154 & 160), were situated where the soils are boggy. In contrast, relevé 161 which is atypical, and where *G. rosmarinifolia* was recorded outside the plot (see Table 3), was located on a more rocky, well-drained substrate.



FIGURE 11.—The *Berzelia intermedia*–*Grubbia rosmarinifolia* Shrublands mainly localized on the south-facing mid-slopes of the Clock Peaks. Note the mid-high *G. rosmarinifolia* forming the overstorey.

Grubbia rosmarinifolia is strongly differential for this community. It forms a mid-high to tall, open to closed shrubland. The understorey may be subdivided into two strata in some stands. In some cases a mid-high open to closed ericoid stratum is found immediately below the tall stratum followed by a closed restioid field layer. In other stands the ericoid and restioid components combine to form a low closed field stratum.

In the samples taken, *Spatalla parilis* (Proteaceae) is restricted to the *Berzelia intermedia*–*Grubbia rosmarinifolia* Shrublands. *Restio arcuatus* together with *Platycaulos compressus* dominates the restioid component and *Erica regerminans* and *E. cubica* form the greater part of the ericoid component.

2.2.3 *Berzelia intermedia*–*Cliffortia grandifolia* Shrublands (G)

Differential species: *Cliffortia grandifolia*, *Senecio hastatus*.

Dominant species: *Cliffortia grandifolia*, *Erica hispidula*, *Penaea cneorum* subsp. *ruscifolia*, *Restio arcuatus*.

Structural formation: Low Closed Ericoid Shrubland with Closed Restioid Understorey and Mid-high to Tall Open Shrubland Overstorey.

Relationships: Keurbos Wet Ericaceous Fynbos (Campbell 1985).

The *Berzelia intermedia*–*Cliffortia grandifolia* Shrubland community (Figure 12) also occurs as part of the *Erica hispidula*–*Berzelia intermedia* Shrubland mosaic. It was sampled mainly on the southeast- to southwest-facing mid-slopes of 12 O'Clock Peak but occurs in patches over an extensive area on the south slopes below the Clock Peaks at elevations from around 600–700 m (above the 'Plaat'). The soils are 'organic phase' Cartref Form.

The community also occurs on the lower north- to northeast-facing slopes below the Clock Peaks, in the Boskloof Valley. These stands are represented by relevé 202 situated near Boskloof Hut at an altitude of about 900 m. Here the soils are of Glenrosa Form.

Cliffortia grandifolia is a striking species. It is a tall, sparingly branched shrub with a thin trunk, often reaching

five metres in height. This species clearly characterizes the community structurally due to its stature and floristically due to its faithfulness. *Cliffortia grandifolia* forms a mid-high to tall open stratum above a low closed graminoid shrubland understorey, dominated by *Erica hispidula* and *Restio arcuatus*. *Penaea cneorum* subsp. *ruscifolia* also contributes significantly to the low stratum (Table 3).

2.3 *Erica hispidula*–*Pentaschistis malouinensis* Shrublands

Differential species: *Pentaschistis malouinensis*.

Dominant species: *Chrysithrix capensis*, *Erica hispidula*, *Tetraria flexuosa*.

Structural formation: Low to Mid-high Closed Graminoid Shrubland.

Relationships: *Simocheilus carneus*–*Restio anceps* Community (Bond 1981); Ruitersberg Wet Ericaceous Fynbos (Campbell 1985).

This community has no differential species, but shares *P. malouinensis* with the *Pentaschistis malouinensis*–*Tetraria bromoides* Shrublands and many other species with communities E–H (see Table 3). These shrublands are distinctly graminoid in character, having an abundance of restios (*Elegia*, *Platycaulos*, *Restio*), grasses (*Pentaschistis*) and sedges (*Chrysithrix*, *Epischoenus*, *Tetraria*). The shrub component is dominated by ericas.

These shrublands are found on north- and south-facing slopes overlooking Boskloof and on north-facing slopes in the Langkuilen Valley at altitudes which range from 770–1 330 m. The gradients of sites sampled ranged from almost level (3°) to moderate (29°). The shallow soils are derived from Peninsula and Goudini Formation sandstone and are classified mainly as Cartref and Mispah Forms. The soil of relevé 188, located at the almost level site, consists of organic material in excess of 0.3 m and was classified as Champagne Form. Rock cover was generally less than 10% except for relevé 172 where 80% was recorded.

The dominant stratum of the *Erica hispidula*–*Pentaschistis malouinensis* Shrublands is a Low Closed Graminoid Shrubland (≤ 1.0 m) with dominance shared between the woody ericoid shrubs, *Erica hispidula* and



FIGURE 12.—The *Berzelia intermedia*–*Cliffortia grandifolia* Shrublands occurring in patches over extensive areas of the south slopes of the Clock Peaks and in Boskloof. Note the characteristic tall, slender *Cliffortia grandifolia*.



FIGURE 13.—The *Pentastichis malouinensis*–*Tetraria bromoides* Shrublands found in Boskloof.

Blaeria coccinea and certain graminoids, particularly *Chrysithrix capensis* and *Tetraria flexuosa*. *Psoralea pinata* and *Widdringtonia nodiflora* occur as sparse emergent shrubs up to 2 m high in some stands.

2.3.1 *Pentastichis malouinensis*–*Tetraria bromoides* Shrublands (J)

Differential species: *Erica pubigera*, *Helichrysum pandurifolium*, *Leucadendron eucalyptifolium*, *Leucadendron salignum*, *Protea aurea*, *Tetraria bromoides*.

Dominant species: *L. eucalyptifolium*, *P. aurea*, *T. bromoides*.

Structural formation: either a Closed Graminoid Shrubland with Mid-high Open Shrubland Overstorey or a Mid-high Closed Shrubland with Tall Mid-dense Proteoid Shrubland Overstorey.

Relationships: *Tetraria bromoides*–*Erica plukenetii* Community (Kruger 1974); *Protea*–*Tetraria* Dry Short Fynbos (Boucher 1978); *Protea aurea*–*Pteridium aquilinum* Community (Bond 1981); Boesmansbos Azonal Restioid Fynbos (Campbell 1985); *Restio inconspicuus*–*Protea aurea* Shrublands (McDonald 1993).

The Cedarberg Formation shales crop out in a narrow band in a west-east direction in the Boskloof Valley. Drainage is to the east and where the shales are exposed, they support stands of the *Pentastichis malouinensis*–*Tetraria bromoides* Shrublands. Three of the sample sites (Relevés 167, 175, 176) were located on shale-derived yellow-brown, Clovelly Form soils with mean pH 3.8 for the A-horizon. The fourth relevé (174) was situated on Glenrosa Form soil (pH 3.6) derived from Nardouw Subgroup sandstone. The estimated mean annual precipitation for the area where these shrublands are found is 800 mm. Elevation ranges from 840–950 m and the gradient from level (4°) to moderate (36°). Vegetation cover is usually high (mean 95%) and mean surface rock cover conversely low at 2.5%.

This community (Figure 13) is classified structurally as Low to Mid-high Closed Graminoid Shrublands with a Mid-high to Tall Open (Proteoid) Shrub Overstorey (see Campbell *et al.* 1981). Floristically these shrublands are not well defined compared with the equivalent community, the *Restio inconspicuus*–*Protea aurea* Shrublands found in the Boosmansbos Wilderness Area (McDonald 1993). In Boskloof, MNR, *Tetraria bromoides* is the most constant differential species with *Protea aurea* and *Leucadendron eucalyptifolium* each found in two of the four plots. *Protea aurea* was most abundant in a sheltered position on the edge of the riparian forest dominated by *Virgilia oroboides* (Relevé 175). The otherwise marked absence of stands of *P. aurea*-dominated vegetation on the Cedarberg shaleband in Boskloof suggests that this serotinous, seed regenerating species may have been adversely affected by past land use régimes (e.g. too frequent or unseasonal fires). *L. eucalyptifolium* is somewhat more common but its distribution is patchy. This could indicate scattered outcropping of shale, but since this species also occurs on sandstones of the Nardouw Subgroup, no clear reason can be given for its local distribution pattern.

2.4 *Erica hispida*–*Hypodiscus aristatus* Shrublands (K)

Differential species: none.

Dominant species: *Cliffortia heterophylla*, *Erica hispida*, *Restio inconspicuus*.

Structural formation: either a Low to Mid-high, Mid-dense to Closed Shrubland or a Mid-high Closed Shrubland with a Low Mid-dense Graminoid Understorey.

Relationships: Nuweberg Mesic Ericaceous Fynbos (Campbell 1985).

This community (Figure 14) is found mainly on north- to northeast-facing slopes of the Clock Peak ridge, overlooking Boskloof, but also on the crest of 10 O'Clock Peak and on north-facing slopes above Langkuilen Valley.



FIGURE 14.—The *Erica hispida*–*Hypodiscus aristatus* Shrublands found on the north- to northeast-facing slopes of the Clock Peak ridge. *Cliffortia heterophylla* dominates the overstorey in this stand.



FIGURE 15.—The *Hypodiscus aristatus*–*Phylica pinea* Shrublands found on the north-facing slopes of Goedgeloof Ridge and on rock outcrops in the Boskloof Valley.

Elevation of the shrublands ranges from about 1 000 m to 1 300 m on moderate slopes with a mean gradient of 27° (24°–28°). Rock cover varies from site to site over a range from 10–80%, with vegetation cover ranging from 70–95%. Estimated annual precipitation is from 800–900 mm.

The A-horizon of the soils have a mean pH 3.4. They are derived from Peninsula Formation and Goudini Formation sandstone and are classified as Cartref Form (Relevés 168 & 170) and Mispah Form (Relevé 181).

As indicated above, the community is structurally variable. The reason for presence of a mid-high closed stratum dominated by *Cliffortia heterophylla* in relevés 168 & 170 is not clear.

The *Erica hispidula*–*Hypodiscus aristatus* Shrubland community is the typical or ‘background’ community of the shrublands where *Cliffortia densa*, *Erica vestita*, *Hypodiscus aristatus*, *Pentameris macrocalycina*, *Stoebe cinerea* and *Thamnochortus cinereus* are common elements (see Table 3). It may be argued that description of the *Erica hispidula*–*Hypodiscus aristatus* Shrublands based on three relevés is tenuous. However, this indicates inadequate sampling, not the non-existence of the community.

2.4.1 *Hypodiscus aristatus*–*Phylica pinea* Shrublands (L)

Differential species: *Ceratocaryum decipiens*, *Phylica pinea*, *Tetraria thermalis*.

Dominant species: *Erica versicolor*, *Phylica pinea*, *Tetraria ustulata*.

Structural formation: Mid-high, Mid-dense Graminoid Shrubland.

Relationships: *Tetraria thermalis*–*Hypodiscus aristatus* Community (Kruger 1974), *Erica viridescens*–*Hypodiscus aristatus* Community (Bond 1981), Nuweberg Mesic Ericaceous Fynbos (Campbell 1985).

This community (Figure 15) is generally Open to Mid-dense Graminoid Shrublands with a Mid-high Open to Closed Ericoid Shrubland Overstorey (see Campbell *et al.* 1981). This community is found on the north-facing slopes of Goedgeloof Ridge and on rock outcrops in the Boskloof Valley. The rocky substrate, with a usual high percentage of boulders and exposed bedrock, results in shallow lithosols (≤ 0.20 m) classified here as Glenrosa and Mispah Forms. In Boskloof the community was sampled at 920 m (Relevés 178 & 201) whereas on Goedgeloof Ridge the mean altitude for the three sample plots (Relevés 193, 197, 198) was 1 173 m. The area sampled by the latter plots is mesic and represents a transition zone from the cooler, moister areas south of Goedgeloof Ridge to the drier lower slopes (see Table 4 and communities P & Q).

Phylica pinea is the most constant differential species in this community. Both *Tetraria thermalis* and *Ceratocaryum decipiens* have a wider distribution on the dry, north-facing slopes (see Table 4), therefore their differential value is diminished. *Erica atropurpurea* is faithful to this community but has a low cover-abundance. Dominance in the mid-high shrub stratum is held by *Erica versicolor*, which typically favours north-facing rocky outcrops (McDonald 1993). The lower stratum does not have a strikingly dominant species but *Tetraria ustulata* does stand out as having a higher cover-abundance than most.

2.4.2 *Hypodiscus aristatus*–*Erica versicolor* Shrublands (M)

Differential species: none.

Dominants: *Edmondia sesamoides*, *Ehrharta setacea* subsp. *scabra*, *Erica hispidula*, *Hypodiscus aristatus*, *Tetraria cuspidata*.

Structural formation: Open to Closed Graminoid Shrubland.



FIGURE 16.—The *Hypodiscus aristatus*–*Restio strictus* Shrublands are found at elevations from 1 200–1 400 m on exposed rocky sites with shallow soil.

Relationships: Nuweberg Mesic Ericaceous Fynbos (Campbell 1985); *Hypodiscus aristatus*–*Erica versicolor* Shrublands (McDonald 1993).

The habitats in which the *Hypodiscus aristatus*–*Erica versicolor* Shrublands and *Hypodiscus aristatus*–*Restio strictus* Shrublands occur are very similar. This is reflected in the structural and floristic similarity of these communities. They differ only in the respective presence and absence of *Erica versicolor* and *Restio strictus* and relative dominance of the graminoid species. The most apparent difference is that the *Hypodiscus aristatus*–*Erica versicolor* Shrublands are found on north-facing slopes as opposed to the south aspect of the *Hypodiscus aristatus*–*Restio strictus* Shrublands. This aspect difference appears to control the presence or absence of *Restio strictus* and *Erica versicolor*, therefore the difference between the communities is subtle.

Dominance of *Hypodiscus aristatus* in the graminoid component is important to note. *Rhodocoma alpina* Linder & Vlok (Restionaceae) a species endemic to this community (H.P. Linder pers. comm.) was not found in any of the relevés but was collected separately.

2.4.3 *Hypodiscus aristatus*–*Restio strictus* Shrublands (N)

Differential species: *Restio strictus*.

Dominants: *Chrysithrix capensis*, *Edmondia sesamoides*, *Erica hispidula*, *Ehrharta setacea* subsp. *scabra*, *Pentstemonis colorata*.

Structural formation: Closed Graminoid Shrubland.

Relationships: Nuweberg Mesic Ericaceous Fynbos (Campbell 1985).

This community (Figure 16) is found at elevations from 1 200–1 400 m. These Low Graminoid Shrublands (<1 m) vary from mid-dense to closed, depending on the locality. They may occur either on exposed rocky sites with shallow pockets of sandy soil or on sites with deeper soil and less rock exposed on the surface. The soils derived from Nardouw Subgroup sandstone vary in depth from 15–30 mm and are classified as Cartref and Mispah Forms. Aspect is mainly south- and southeast-facing, on slopes with a moderate gradient (mean 16°). The community receives an estimated mean annual precipitation of 1 000–1 200 mm, the soils are highly leached and litter accumulation is low.

This community is distinct and well differentiated by *Restio strictus*. Although ericoid shrubs are well represented, the graminoid nature of the *Hypodiscus aristatus*–*Restio strictus* Shrublands stands out. *Ehrharta setacea* subsp. *scabra*, *Pentstemonis colorata* and *Chrysithrix capensis* dominate with *Restio inconspicuus* and *Restio strictus* and various sedges playing a subordinate role. *Ursinia trifida* has low cover-abundance but is remarkably constant in the relevés and it is interesting to note the presence of *Erica daphniflora*. Notable absences are *Lobelia neglecta*, *Psoralea pinnata* and *Kniphofia uvaria*, but of prime importance is the absence of *Erica versicolor*. This absence distinguishes the community from the *Hypodiscus aristatus*–*Erica versicolor* Shrublands.



FIGURE 17.—The *Hypodiscus aristatus*–*Erica multumbellifera* Shrubland found on the north slopes of Goedgeloo Ridge.

2.4.4 *Hypodiscus aristatus*–*Erica multumbellifera* Shrublands (O)

Differential species: *Erica multumbellifera*, *Staberoha cernua*.

Dominant species: *Erica melanthera*, *Staberoha cernua*, *Tetraria ustulata*.

Structural formation: Closed Graminoid Shrubland.

Relationships: some affinities to the Acid Sand Flats Community (Boucher 1978).

The description of this community (Figure 17) is based on two relevés, 194 & 195. This small sample size places a question on the validity of this community concept but since it is distinctly different from all other communities described, it is retained for completeness. These shrublands show affinity to the shrublands of high elevation on shallow soils (Table 3).

The *Hypodiscus aristatus*–*Erica multumbellifera* Shrublands were sampled at 1 180 and 1 300 m on the north slopes of Goedgeloo Ridge. The sites were almost level with a mean gradient of 6°. The Cartref Form soils were 0.2–0.4 m deep and almost no rock was exposed on the surface. Litter was very low and vegetation cover exceeded 95%.

Relevé 194 had a more abundant graminoid component than Relevé 195, whereas *Erica melanthera* was more abundant in the latter sample. Presence of *E. melanthera* suggests impeded drainage in the soil, and a possible explanation for the existence of this community is wet soil conditions for part of the year and extremely dry soil for the remainder. This would preclude species intolerant of such conditions. A similar regime was found by Boucher (1978) in the 'Acid sand flats communities' where *Erica multumbellifera* was also found. Further sampling of the *Hypodiscus aristatus*–*Erica multumbellifera* Community over a wider range may provide more information about the habitat factors determining the distribution of this community.

This community is transitional between the communities of the cool, moist high elevations and those of the highly insolated, drier north-facing slopes of Goedgeloof Ridge described below. The transition is reflected in the species shared with both groups of communities.

3. *Leucadendron eucalyptifolium* Shrublands of the extreme north slopes

The two shrubland communities included in this section show strong floristic affinities to the shrublands on the lower south slopes on the sample transect. This is most likely due to the apparent equivalent nutrient status of the soils of the two extreme ends of the transect. Further investigation of these respective communities and their underlying environmental relationships is necessary before this hypothesis can be conclusively tested.

3.1 *Leucadendron eucalyptifolium*–*Erica melanthera* Shrublands (P)

Differential species: *Erica melanthera*, *Penaea cneorum* subsp. *ruscifolia*, *Psoralea pinnata*, *Staberoha cernua*, *Ursinia nudicaulis* (i.e. species occurring in at least three of four relevés).

Dominant species: *Leucadendron eucalyptifolium*, *Tetraria ustulata*.

Structural formation: Open to Closed Graminoid Shrubland with Mid-high to Tall Open Proteoid Shrubland Overstorey.

Relationships: *Protea neriifolia*–*Leucadendron eucalyptifolium*–*Erica triceps* Community (Bond 1981); Robinson Mesic Proteoid Fynbos (Campbell 1985).

This community (Figure 18) is found on the moderately steep (22°) north-facing slopes of Goedgeloof Ridge between 800–1 060 m. They are found mostly on shallow Glenrosa Form soils, but one notable exception was relevé 150 where the soil was sandy, 1.5 m deep with a bleached E-horizon and a podzolised B-horizon. This localized soil



FIGURE 18.—The *Leucadendron eucalyptifolium*–*Erica melanthera* Shrublands are found on the moderately steep north-facing slopes of Goedgeloof Ridge.



FIGURE 19.—The *Leucadendron eucalyptifolium*–*Hypodiscus argenteus* Shrublands found in a mosaic with the *Leucadendron eucalyptifolium*–*Erica melanthera* Shrublands on the moderately steep north-facing slopes of Goedgeloof Ridge.

was classified as Lamotte Form, which is exceptional for this area. Surface rock cover is highly variable, ranging from 6–85% and the habitat is well drained.

As delimited here, the *Leucadendron eucalyptifolium*–*Erica melanthera* Shrubland is not floristically clearly defined. It appears that although a community definition is possible, the community represents fragments of two or perhaps more undersampled and undefined communities. They are grouped together by virtue of commonness of a few widespread 'differential' species but the 'strings' of single occurrences in Table 4 support the above conclusion. As defined, the community shows affinity to the communities of the lower south slopes and the high elevation zone described above under sections 1–3. However, high cover-abundance of *Leucadendron eucalyptifolium* and presence of *Elegia galpinii*, *Hypodiscus striatus* and *Anomalanthus scoparius* clearly place this community apart from those described above.

The *Leucadendron eucalyptifolium*–*Erica melanthera* Shrublands have two strata. The dominant stratum is an Open to Closed Graminoid Shrubland which does not exceed 1 m in height. Above this is an overstorey of *Leucadendron eucalyptifolium* (proteoid shrubs) which varies from open to mid-dense and from mid-high to tall (1–>2 m).

3.2 *Leucadendron eucalyptifolium*–*Hypodiscus argenteus* Shrublands (Q)

Differential species: *Heteropogon contortus*, *Hypodiscus argenteus*, *Lanaria lanata*, *Lobelia capillifolia* (i.e. species with four or more occurrences in five relevés).

Dominant species: *L. eucalyptifolium*, *Tetraria ustulata*, *Restio filiformis*.

Structural formation: Open to Closed Graminoid Shrubland with Mid-high Open Proteoid Shrubland Overstorey.

Relationships: in part, this community is equivalent to the *Phylla axillaris*–*Felicia filifolia* Community (Ruitersbos) and *Passerina obtusifolia*–*Felicia filifolia* Community (Swartberg) of Bond (1981) and Sebrafontein Dry Asteraceous Fynbos (Campbell 1985).

This community is found on the moderately steep north-facing slopes of Goedgeloof Ridge, in a mosaic with the *Leucadendron eucalyptifolium*–*Erica melanthera* Shrubland at elevations from 680–900 m. The soils, derived from Nardouw Subgroup sandstone, are classified as Glenrosa and Mispah Form. Surface rock cover exceeds 90% in all relevés representing this community but despite this there is considerable vegetation with a mean projected canopy cover of 78%. Estimated mean annual precipitation is 700–800 mm.

In the *Leucadendron eucalyptifolium*–*Hypodiscus argenteus* Shrublands (Figure 19), *Leucadendron eucalyptifolium* does not exceed 1.2 m and in two relevés (185 & 186), *Leucospermum calligerum* is the dominant proteoid in the overstorey. The upper stratum varies from a Mid-high Open to Tall Open Proteoid Shrubland and the lower (dominant) stratum varies from an Open to a Closed Graminoid Shrubland.

There are a number of affinities between this Community and the communities of the lower south slopes of the Langeberg above Swellendam. Equally there are numerous similarities between the *Leucadendron eucalyptifolium*–*Hypodiscus argenteus* Shrublands and the *Cannomois parviflora* Shrublands north of Grootberg (McDonald 1993). The *Leucadendron eucalyptifolium*–*Hypodiscus argenteus* Shrublands are mesic in character but may once again be represented by a group of relevés which through commonness are associated but which may truly be fragments of other communities, e.g. part of the more arid *Passerina obtusifolia*–*Leucospermum calligerum* Shrublands. This requires further clarification.

DISCUSSION AND CONCLUSIONS

The classification presented in this study was developed from a phytosociological perspective but with management of the fynbos shrublands of the Langeberg in mind (McDonald 1993). Some of the units defined are limited in extent, and from a management viewpoint it would not be practical to treat them separately from broader vegetation units. However, since the classification is hierarchical, similar communities are grouped together according to the level of the hierarchy. It is therefore possible for any manager of the fynbos shrublands of the Langeberg to select the appropriate level required for any particular management treatment. Those communities grouped at the same level may then be treated similarly.

Two problems have been encountered with the methods used in this study. Firstly, since no initial stratification of aerial photographs of the study area was done, some communities were undersampled. There is no satisfactory way of detecting this before analysis of the data. Both the TWINSpan and Braun-Blanquet methods of classification have indicated communities that have been undersampled. The most obvious is the *P. malouinensis*–*Tetralix bromoides* Shrubland found on the Cedarberg

shaleband. Another example is the *Hypodiscus aristatus*–*Erica multumbellifera* Shrubland for which a description is given. Ideally this community requires further sampling upon which an adequate description may be based. Fragments of communities recognized in other parts of the Langeberg are included in the *L. eucalyptifolium* Shrublands of the extreme north slopes of the transect. In the TWINSpan analysis this was shown by relevés 185 and 186 being separated from relevés 151, 183, 184 and 199 (see also Table 4). Further sampling would clarify whether this is due to too few samples or that the communities are simply poorly represented in this part of the Langeberg. It was not possible to obtain further samples of these communities in this study because the area had been burnt soon after the initial samples were taken.

It may be argued that a community may be characterized by one or two species whose presence is a result of differential post-fire recruitment (Van Wilgen *et al.* 1992). This possibility would increase if the sample size for a given community is small, which in turn could lead to an artificial classification. However, each community is not based solely on the character species but is based on a specific combination of species for each community. These combinations should be seen as the key to identifying each community.

The complexity of the metamorphosed Malmesbury Group sediments that occur below the 'Plaat' is reflected in the vegetation occurring in this part of the MNR. Here fynbos communities characterized by constant presence of *Cliffortia serpyllifolia* are found on soils derived from quartzites and shales. The Afromontane forests also occur on the Malmesbury Group shales, but in this case in moist kloofs.

Although it has been stated that *P. aurea* may be used as a 'marker', indicating the position of the Cedarberg Formation shales in the folded strata along the length of the Langeberg (McDonald 1993), this is a misconception. A large stand of fynbos dominated by *P. aurea* is found at the base of 10 O'Clock Peak, below the 'Plaat', on Malmesbury shale-derived soil. The response of *P. aurea* is therefore to the fine-textured shale-derived soils with higher nutrient status, regardless of their lithological origin or stratigraphic position.

The vegetation of the MNR appears more complex than that of the Boosmansbos Wilderness Area (BWA) (McDonald 1993). This could be ascribed to more complex environmental gradients and a greater diversity of habitats. However, detailed analysis of environmental data is needed to substantiate such a claim.

No equivalent of the *Restio inconspicuus*–*Leucadendron eucalyptifolium* Shrubland which is widespread in BWA is found in the MNR. The *Restio inconspicuus*–*Anthochortus crinalis* Shrublands of BWA and the *Erica hispidula*–*Berzelia intermedia* Shrublands of MNR are essentially similar. The communities on the Cedarberg Formation shale of the two areas are similar except that the *Pentaschistis malouinensis*–*Tetralix bromoides* Shrubland is poorer in species. The *Cliffortia serpyllifolia* Shrublands of the lower south slopes of MNR have no equivalent in BWA. The reason for the absence of these shrublands or their equivalent in BWA is not clear but it may be due

to the absence of shale-derived soils on the lower south slopes of the BWA transect.

The *Cannomois parviflora* Shrublands of BWA are represented in part by the *Leucadendron eucalyptifolium* Shrublands of the extreme north slopes of the MNR transect, but more extensive sampling and more detailed analysis is necessary to clarify the classification of these communities.

Communities identified in different studies from different mountain ranges can not be simply equated (McDonald 1993). At the landscape scale there does not appear to be much difference between the fynbos vegetation of the Marloth Nature Reserve and the Boosmansbos Wilderness Area (McDonald 1993). Apparent differences are more at the level of communities which are micro-habitat related. Closer examination is therefore required of (i) the patterns of distribution of communities on the Langeberg and (ii) the high turnover of species between communities and landscapes on the Langeberg. This is beyond the scope of the present paper but forms a principal part of further detailed analyses of the vegetation and flora of the Langeberg (McDonald unpublished).

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BOTHALIA

Volume 23,1

May/Mei 1993

CONTENTS—INHOUD

1. Studies in the Ericoideae (Ericaceae). XII. The placing of the genus <i>Blaeria</i> into synonymy under <i>Erica</i> ; nomenclatural and taxonomic changes for the southern African region. E.G.H. OLIVER	1
2. Studies in the Ericoideae (Ericaceae). XIII. Three new species of <i>Erica</i> from the southwestern Cape. E.G.H. OLIVER	9
3. The hepatics, <i>Symphyogyna podophylla</i> and <i>Pallavicinia lyellii</i> (Pallaviciniaceae) in southern Africa. S.M. PEROLD	15
4. A biosystematic study of <i>Pentameris</i> (Arundineae, Poaceae). N.P. BARKER	25
5. Studies in the Marchantiales (Hepaticae) from southern Africa. 1. The genus <i>Dumortiera</i> and <i>D. hirsuta</i> ; the genus <i>Lunularia</i> and <i>L. cruciata</i> . S.M. PEROLD	49
6. <i>Panicum simulans</i> (Paniceae, Poaceae), a new species from southern Africa and its leaf anatomy. L. SMOOK and R.P. ELLIS	59
7. Notes on African plants:	
Allisoniaceae. The hepatic, <i>Calycularia crispula</i> (Metzgeriales) reported from Malawi and Zambia. S.M. PEROLD	79
Asteraceae. An evaluation of Hutchinson's 'beetle-daisy' hypothesis. J.J. MIDGLEY	70
Fabaceae. <i>Vigna kokii</i> , a new species from southern Africa. B.J. PIENAAR	68
Fabaceae. Notes on the genus <i>Argyrolobium</i> (Crotalariaeae) including a new species from southern Africa. T.J. EDWARDS	77
Oxalidaceae. A new species of <i>Oxalis</i> from the western Cape. E.G.H. OLIVER	72
Pteridophyta—Adiantaceae. A new cytotype for <i>Acrostichum aureum</i> . J.P. ROUX	75
Rosaceae. Observations on <i>Cliffortia micrantha</i> . A.C. FELLINGHAM	65
Rosaceae. <i>Cliffortia fasciculata</i> , a superfluous name for <i>C. amplexistipula</i> . A.C. FELLINGHAM	67
8. First report on the presence of <i>Enterobryus</i> species (Trichomycetes: Eccrinales) in South Africa and the description of three new species. G.J.M.A. GORTER	85
9. Mycorrhizal status of plants growing in the Cape Floristic Region, South Africa. N. ALLSOPP and W.D. STOCK	91
10. Pollen morphology of <i>Curroria</i> , <i>Mondia</i> , <i>Socotranthus</i> and <i>Stomatostemma</i> (Periplocaceae). R.L. VERHOEVEN and H.J.T. VENTER	105
11. Dynamics of the forest vegetation of the Umtiza Nature Reserve, East London. J.J. MIDGLEY and P.N. GOBETZ	111
12. The vegetation of the northeastern Orange Free State, South Africa: physical environment and plant communities of the Ea land type. H.C. ECKHARDT, N. VAN ROOYEN and G.J. BREDEN-KAMP	117
13. The vegetation of the southern Langeberg, Cape Province. 1. The plant communities of the Boosmansbos Wilderness Area. D.J. MCDONALD	129
14. The vegetation of the southern Langeberg, Cape Province. 2. The plant communities of the Marloth Nature Reserve. D.J. MCDONALD	153

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